Fauna of New Zealand

Ko te Aitanga Pepeke o Aotearoa

Naturalised terrestrial Stylommatophora
(Mollusca: Gastropoda)

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Manaaki
Whenua
P R E S S

Class **Mollusca**
Order **Gastropoda**

Naturalised terrestrial slugs and snails

Gastropods, or slugs and snails, are a very diverse group of molluscs. Most are marine, but many occur in freshwater and terrestrial habitats. Worldwide, terrestrial gastropods have been estimated to number about 35 000 species. New Zealand's indigenous terrestrial gastropod fauna is among the richest in the world, with an estimated 1350 species. However, of the estimated global diversity of 71–92 families only 11 are represented in New Zealand's indigenous fauna.

Through human activities, many species of terrestrial gastropod have been spread to and naturalised in areas outside their original range. Often these species have become pests in their new homes due to their damage to cultivated crops, their role in the transmission of parasitic diseases that affect humans and livestock, or their adverse effects on indigenous flora and fauna.

Our naturalised terrestrial gastropod fauna currently comprises 29 species, representing 15 families that were not part of the original New Zealand fauna. These species originate in Europe, North America, or the Pacific; some may have been introduced secondarily from populations first naturalised elsewhere. The species established in New Zealand are associated with man and his crops in their native range, with great propensity for passive dispersal, and have been widely distributed through human commerce. Several species established in New Zealand so early during the period of European settlement that zoologists of that time thought them to be members of the native mollusc fauna.

The general body plan in most terrestrial gastropods comprises the conical visceral mass coiled into a spiral within a single shell, and the head-foot which outwardly comprises a ventral muscular pad for locomotion and anteriorly a mouth and two pairs of tentacles. These

(continued overleaf)
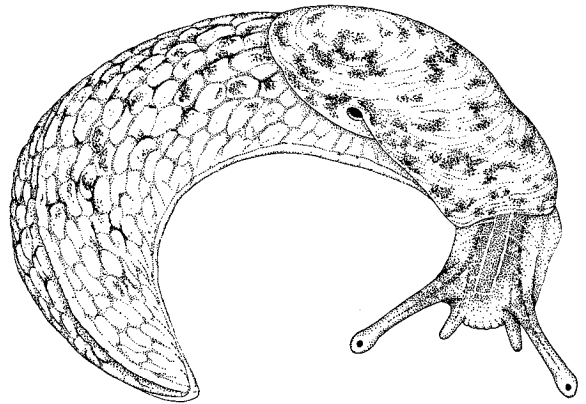
Illustration / Whakaahua: The grey field slug, *Deroceras reticulatum* (Müller) (Illustrator / Kaiwhakaahua: G.M. Barker).

Ko tēnei mea, te wae-uaua, arā, te 'gastropod', he rōpū whānui tonu nō te karangatanga e kīia nei he 'hanga-mohe'. Arā ngā tino tauira o te wae-uaua, ko te ngata me te pūtoko. Ko te nuinga, ka noho ki te moana, engari arā anō ētahi ko ngā wai māori, ko te whenua tonu rānei tō rātou kāinga noho. O ngā hanga-mohe e noho ana ki uta, e whakapaetia ana kei te āhua 35 000 ngā momo, huri i te ao. Ā, ko ō Aotearoa taketake ake tētahi o ngā huinga huhua noa, inā hoki, e whakapaetia ana ko tōna 1350 ngā momo hanga-mohe ko Aotearoa tō rātou kāinga tūturu. Heoi anō, o ngā whānau hanga-mohe āhua 71–92 nei, puta noa i te ao, 11 noa iho nō Aotearoa, taketake ake.

Nā ngā mahi a te tangata, kua tae atu ētahi wae-uaua noho whenua ki ētahi wāhi o te ao i tua atu i ō rātou kāinga ake, ā, kua rarau tā rātou noho i reira. I ētahi wā kua riro ngā mea nei hei hoariri i ō rātou kāinga hou, i te mea nā rātou kua hē pea te tipu o ngā māra kai, kua rere rānei ētahi mate pirinoa i a rātou, kua tau ki runga i te tangata, i ā rātou kararehe rānei, tērā rānei kua patua, kua tāmia e rātou ngā kararehe me ngā tipu māori o ō rātou kāinga hou.

E 29 ngā momo wae-uaua noho whenua o wāhi kē kua tau tā rātou noho i Aotearoa, nō ngā whānau tekau mā rima. I takea mai ēnei momo i Ūropi, i Amerika ki te Raki, i Te Moana-nui-a-Kiwa rānei, ā, tērā pea i tau atu ētahi ki whenua kē i te tuatahi, ka noho āhua 'tangata whenua' mai i reira, kātahi ka kawea mai ki Aotearoa. Ko ngā momo kua rarau tā rātou noho i Aotearoa, e kaha noho ana a Ingāmāra me ngā mahinga ahuwhenua a te

(ara haere tonu)

molluscs, commonly known as snails, are able to completely retract their head-foot into the shell for protection from desiccation and from predators. Features of the shell, and of the external morphology and internal anatomy of the head-foot, are important in the identification of snails. There are 15 species of snail in our naturalised fauna.

In the moist and humid conditions that prevail in many regions of the world, the ability to retract into a protective shell has been less important, and many groups of terrestrial gastropods have evolved forms with a reduced shell. In the initial stages of this evolution the shell is carried on the animal's back, but is no longer able to fully protect the entire animal. Animals at this stage of evolution, commonly known as semi-slugs, are represented in our naturalised fauna by a single species.

In the more advanced stages of this evolution the shell is reduced to a small plate or granules enclosed within the head-foot tissues, or lost completely. These animals, known as slugs, are simply snails with a reduced shell, and their identification is more dependent on the external morphology and internal anatomy of the head-foot. There are 14 species of slug in our naturalised fauna.

Contributor **Gary Barker** was born in Matamata, Waikato, but spent his youth on a farm surrounded by bush-clad hills in the Bay of Plenty. It was there that he developed an interest in wildlife, and invertebrates in particular. In 1972 Gary joined the Ministry of Agriculture at Ruakura Agricultural Research Centre. While working as a technician he obtained a New Zealand Certificate in Science at Waikato Polytechnic. Over a period of 24 years Gary published more than 100 papers on population and community ecology of invertebrates in agricultural systems. He has worked extensively with farmers and other researchers, in New Zealand and internationally, to develop sustainable pest management practices. In recognition of this contribution, in 1985 Gary was appointed as a senior research scientist with the Ministry of Agriculture. He also developed research interests and published in biogeography, systematics, and ecology of indigenous invertebrats, especially terrestrial molluscs. In 1996 he joined Landcare Research as a research scientist. His work is now centred on the systematics and community ecology of New Zealand indigenous invertebrates, and broader questions of biodiversity assessment.

tangata, otirā, ko ērā e rite ana ngā kai o roto ki ērā o ō rātou wā kāinga. Ā, nā te piri tahi ki ngā tipu, kua kawea haeretia ngā wae-uaua nei e te tangata ki ngā tōpito o te ao tauhokohoko. Nā te tere rarau o te noho a ētahi i muri tonu i te taenga mai o te Pākehā ki konei, ka pōhēhē ngā kaimātai kararehe o ērā wā nō Aotearoa tūturu aua nanakia rā.

Ko te tinana o te nuinga o ngā wae-uaua noho ki uta, he koeko te hanga o te wāhi kei reira ngā whēkau, ā, e takoto raungaiti mai ana, pēnei i te pītau nei, ki roto i tētahi anga. Arā anō te 'ūpoko-waewae'. Ki te titiro atu koe ki te mea nei, ko te wae-uaua kei raro iho. Mā te wae-uaua, ka taea e te mea nei te nekeneke haere. Kei mua i tēnei wāhanga, ko te waha me ngā weri e whā e noho takirua mai ana. Ko tēnei hanga-mohe e whakamāramatia ake nei, ko ia anō te ngata e mōhio nei tātou katoa. Ka taea anō e te ūpoko-waewae te hoki ki roto i te anga kia kore ai ia e pakoko noa, e kainga rānei e te hoariri. Ko te āhua o te anga, ko te hanga whakawaho o te ngata, me te hanga whakaroto o te ūpoko-waewae, koinei katoa ngā mea ka āta tirohia e whakatauhia ai ngā rerekētanga i waenganui i tēnā, i tēnā momo ngata. O ngā kararehe manene katoa kua pūmau tā rātou noho i Aotearoa, 15 ngā momo ngata.

I ngā takiwā o te ao e kaha tonu ana te hauwai me te pūmahana, kua kore i tino hiahiatia te anga hei whakamarumaru i ngā hanga-mohe e noho ana i reira, ā, i roto i ngā tau mano tini, kua iti ake ngā anga o ētahi. Ki te tirohia ētahi momo wae-uaua kua tīmata tā rātou takahi i tēnei huarahi, ka kitea e waha tonu ana rātou i ō rātou anga, engari kua kore e taea te uru katoa atu ki roto i taua anga hei ārai atu i ngā kino. Ko ngā wae-uaua pēnei, ka kīia ki te reo Ingarihi he 'hāwhe-pūtoko', arā, kei waenga i te ngata me te pūtoko. O ngā momo wae-uaua o tāwāhi kua tatū tā rātou noho i Aotearoa, kotahi anake e pēnei ana te āhua.

Ko ngā mea kua roa tonu e takahi ana i te huarahi e ngaro atu ai ō rātou anga, tērā pea he papa hangariki noa iho te anga, tērā rānei kua noho noa mai ētahi kongakonga o te anga ki roto i te kiko o te ūpoko-waewae, tērā tonu rānei kua kore katoa. Ki te pēnei te āhua, kua kīia he pūtoko, engari he ngata tonu kē, heoi anō te rerekētanga, kua iti noa ake te anga, kua kore katoa rānei. Hei whakatau i ngā rerekētanga i waenganui i ēnei momo wae-uaua, me āta titiro ki te hanga whakawaho, tae atu ki te hanga whakaroto o te ūpoko-waewae. Tekau mā whā ngā momo pūtoko kua āhua tangata whenua tā rātou noho i Aotearoa i roto i ngā tau.

I whānau mai te kaituhi nei, a **Gary Barker**, i Matamata, i roto o Waikato. Heoi anō, i tana taiohinga, noho ai ia ki tētahi pāmu e karapotia ana e te ngahere i te rohe o Te

Moana a Toi. Nō reira mai tana ngākau nui ki ngā mea oreore o te wao nui a Tāne, me tana aro nui anō ki ngā mea tuarā-kore. I te tau 1972 ka whai mahi a Gary i te Manatū Ahuwhenua, i te Pūtahi Rangahau Ahuwhenua o Ruakura. I a ia e mahi ana hei ringa hangarau, ka whakawhiwhia ia ki tana Tiwhikete o Aotearoa mō te Pūtaiao, mai i te Kuratini o Waikato. I roto i te 24 tau, neke atu i te 100 ngā tuhinga kua whakaputaina e Gary e pā ana ki te maha me te āhua o te noho tahi a ngā hanga tuarā-kore i roto i ngā pūnaha ahuwhenua. Kua kaha tonu tana mahi tahi ki te hunga ahuwhenua me ētahi atu kairangahau, i tēnei whenua me tāwāhi anō hoki, kia takoto mai ai ētahi tikanga nanati i ngā kararehe takakino. Nā ēnei mahi āna, i te tau 1985 ka whiwhi a Gary i tētahi tūranga mō te kairangahau pūtaiao matua i te Manatū Ahuwhenua.

Kua whāwhā atu anō hoki ia i ētahi atu momo mātauranga, pēnei i te koiora-matawhenua, i ngā whakapapa me ngā pūnaha whakarōpū i te ao o Tāne, me te āhua o te noho tahi a ngā hanga tuarā-kore o Aotearoa tūturu ki ō rātou ake taiao. I tēnei kaupapa whakamutunga, ko ngā hanga-mohe noho ki uta ngā mea i āta tirohia e ia. I tua atu i ngā mahi rangahau, kua whakaputa tuhinga anō ia e pā ana ki ēnei kaupapa. I ēnei rā, e āta whakapau kaha ana ia ki ngā whakapapa, ngā pūnaha whakarōpū, me te āhua o te noho tahi a ngā hanga tuarā-kore tūturu o Aotearoa ki ō rātou taiao, tae atu ki te aromatawai i ngā huhua a Tāne.

He Kupu Āwhina — Glossary

aromatawai i ngā huhua a Tāne —
              biodiversity assessment (land-based)
hanga-mohe — soft-bodied > mollusc
koiora-matawhenua — biogeography
pūtoko — slug
pakoko — desiccated
papa hangariki — small plate
pītau — circinate frond of a fern > spiral
ringa hangarau — technician
tikanga nanati i ngā kararehe takakino — pest
                           management
weri — tentacle
wae-uaua — muscular foot, gastropod

Translation by **H. Jacob**
Huatau Consultants, Wellington

* *

TRIBUTE

Cleveland Tymone DUVAL
8 November 1942 – 8 June 1998

New Zealand science lost a very experienced editor when **Tymone Duval,** after having been in remission for some months, died suddenly from acute lymphoblastic leukemia.

Tymone had been the series editor for the *Fauna of New Zealand* since its inception in 1982, and edited all 37 numbers published up until the time of his death. Even when on sick leave in 1998 he continued to bring this present work and other contributions closer to completion.

Tymone joined the Department of Scientific and Industrial Research (DSIR) as a science editor in 1973, with particular responsibility for the *New Zealand Journal of Zoology.* Previously he worked on insect control projects in Zambia (1965–68) and Botswana (1970–72), and was an editor for *PANS (Pest Articles and News Summaries)* (1969–70).

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ABSTRACT

The naturalised terrestrial gastropod fauna of New Zealand is shown to comprise a total of 29 species representing 11 stylommatophoran families. Taxa previously recognised in New Zealand's naturalised fauna and confirmed in this study are (with recommended common names): Agriolimacidae – *Deroceras laeve* (marsh slug), *D. panormitanum* (brown field slug), *D. reticulatum* (grey field slug); Arionidae – *Arion hortensis* (Férussac's orange soled slug), *A. intermedius* (glade slug); Cochlicopidae – *Cochlicopa lubrica* (slippery moss snail); Ferussaciidae – *Cecilioides acicula* (blind pin snail); Helicidae – *Cantareus aspersus* (brown garden snail); Hygromiidae – *Candidula intersecta* (wrinkled snail); Limacidae – *Lehmannia nyctelia* (Bourguignat's slug), *Limacus flavus* (yellow cellar slug), *Limax maximus* (tiger slug); Milacidae – *Milax gagates* (jet slug), *Tandonia budapestensis* (Budapest slug), *T. sowerbyi* (Sowerby's slug); Pupillidae – *Lauria cylindracea* (chrysalis snail); Testacellidae – *Testacella haliotidea* (shelled slug); Valloniidae – *Vallonia excentrica* (eccentric grass snail); Vertiginidae – *Vertigo ovata* (grassland whorl snail); Zonitidae – *Oxychilus alliarius* (garlic glass snail), *O. cellarius* (cellar glass snail), *O. draparnaudi* (Drapamaud's glass snail), *Vitrea crystallina* (crystal snail). Consistent with recent revisions, several generic–species epithet combinations are applied for the first time to the New Zealand naturalised fauna: these include *Cantareus aspersus* (formerly in genus *Helix*); *Limacus flavus* (formerly in *Limax(Limacus)* or *Lehmannia*); *Tandonia budapestensis* and *T. sowerbyi* (formerly *Milax*).

Arion distinctus* (Arionidae) (Mabille's orange soled slug) is shown to have been long established and widespread in New Zealand, but previously not recognised as a component of *A. hortensis* s.l. *Zonitoides arboreus* (Zonitidae) (orchid snail) is formally recorded as a naturalised species, although its presence since the 1950s has been recognised in the popular press and unpublished plant protection records. *Helicodiscus singleyanus* (Helicodiscidae) (Singley's subterranean discus snail) is recorded in the naturalised fauna for the first time with recognition of the presumedly indigenous species *Hydrophrea academia* as a new junior synonym; this small, largely subterranean species has been known from widely scattered localities since 1970. *Lehmannia valentiana* (Limacidae) (Valencia slug) is recorded in New Zealand for the first time, although specimen material indicates that it has been established at various localities in the North Island since the 1970s. *Prietocella barbara* (Hygromiidae) (banded conical snail) is formally added to the naturalised fauna, although its establishment was recorded in 1983 but not published; this species is rapidly spreading through northernmost New Zealand. *Coneuplecta calculosa* (Euconulidae) (calculus cone snail) is the species most recently confirmed (1995) as a naturalisation, and is known at present from a single locality.

Family and generic diagnoses are presented; these were initially developed from the literature, but incorporate much new anatomical observation. All species are redescribed and illustrated on the basis of conchological and anatomical observations of New Zealand and extralimital material, with new or corrected anatomical data, and haploid chromosome numbers taken from the literature. The systematic status of each species is discussed, and information is presented on their distribution, history in New Zealand, and biology. A key to their identification is included. Methods for collection, preparation, and curation of these molluscs are briefly outlined. The systematic treatment of the taxa and the key are supported by a comprehensive description and discussion of the body plan and organ systems in Stylommatophora that are important in systematics and in taxon recognition. Most species are illustrated from life in a series of colour plates.

CHECKLIST OF TAXA

CONTENTS

ACKNOWLEDGMENTS

INTRODUCTION

New Zealand has a large and phylogenetically diverse indigenous terrestrial mollusc fauna, most species of which are dependent on undisturbed forest or tussock grassland as habitat. In species number and sympatric diversity, the New Zealand indigenous terrestrial mollusc fauna is among the richest in the world per unit land area (Solem *et al.* 1981, Solem 1984b, Emberton 1994a), with an estimated 1350 species. This indigenous terrestrial fauna contains one neritopsinan family (Hydrocenidae) and one caenogastropod family (Liareidae) but, as in most

other regions of the world, is dominated by stylommatophoran Pulmonata.

The indigenous fauna is supplemented by a small and continually expanding naturalised fauna of Stylommatophora, which is the focus of this publication. These naturalised species are the slugs and snails familiar to the general public. There is little appreciation, however, of the number and phylogenetic diversity of species represented in the naturalised fauna, or of the extent to which they have pervaded the New Zealand landscape. They form an important element of the New Zealand biota, particularly in modified habitats.

The naturalised terrestrial mollusc fauna currently comprises 29 species, representing no less than 15 families of Stylommatophora. These species originate in Europe, North America, or the Pacific, although some may have been introduced secondarily from stock first naturalised elsewhere (Barker 1992). The species established in New Zealand are those which are synanthropes in their native range, with great propensity for passive dispersal, and which have been widely distributed through the activities of man.

Methods and conventions

A considerable part of this contribution is based on material gathered from the field throughout New Zealand. Many people contributed specimens, as acknowledged under Material Examined for each species. Specimen localities without a collector's name are those collected by the author. Detailed specimen collection records and distribution maps are presented for each species so as to be of value to later students of New Zealand's naturalised fauna.

For specimens collected in New Zealand, the two-letter codes at the beginning of each locality record or group of similar records alludes to the areas designated by Crosby *et al.* (1976, 1998), mapped on p. 248.

Unless otherwise indicated, material is deposited in the private collection of the author. Abbreviations for institutional repositories are as follows:

AMNZ Auckland Museum, Auckland, N.Z.
AMSA Australian Museum, Sydney, Australia
ANSP Academy of Natural Sciences, Philadelphia, U.S.A.
BMNH The Natural History Museum, London, U.K.
BPBM Bernice P. Bishop Museum, Honolulu, Hawaii
CMNZ Canterbury Museum, Christchurch, N.Z.
MONZ Museum of New Zealand, Wellington, N.Z.
NHMW Naturhistorisches Museum, Vienna, Austria
OMNZ Otago Museum, Dunedin, N.Z.

Initial specific determinations were made by reference to the literature. Identifications were confirmed by European and North American malacologists (see Acknowledgments) and, for many species, by examination of material from the species' native range collected by the author or gifted by colleagues. The family and generic diagnoses were initially developed from the literature, but incorporate much previously unpublished anatomical observation. The species descriptions and illustrations presented are based entirely on conchological and anatomical observations of the author, and for many species include new or corrected information.

Names of genera and species quoted in synonymy refer to world material, and include New Zealand synonyms (some new), as discussed in the text. These synonyms have been taken from the literature, without critical evaluation, unless otherwise noted.

The literature pertaining to most species is very extensive, but for the greater part is not readily available in New Zealand. It has not been possible owing to space limitations to provide a comprehensive list of references for each species, but a synopsis with key references is provided under Remarks. Furthermore, listings of junior synonyms for genera and species are supported by bibliographic references, to facilitate navigation through the often complex nomenclatural history of these taxa.

The category 'of authors' is included in these lists to indicate the generic placements (often) extensively used in the older literature, but which were subsequently shown to be inconsistent with generic limits as defined by type species. For example, *Helix* Linnaeus, 1778 was once applied as the generic name for the majority of terrestrial snails, but following the designation by de Montfort (1810) of *Helix pomatia* Linnaeus, 1758 as type species, *Helix* was subsequently applied in a more restricted sense.

Public awareness of gastropods is facilitated by the use of common names. For each species recognised in the naturalised fauna, a common name is recommended. In general, if there was a name well established overseas (e.g., Godan 1983, Gittenberger *et al.* 1984) or in New Zealand (e.g., Ferro *et al.* 1977, Foord 1990) it was given priority. Where new common names were required, or where a choice was required between two or more common names in use, preference was given to names:
(i) based on a translation of the specific epithet,
(ii) descriptive of the animal or its habitat, and/or
(iii) informative about its origin or nomenclatural history.

Chromosome numbers were taken from the literature, namely Perrot (1938), Beeson (1960), Burch & Heard (1962), Laws (1965, 1966), Rainer (1967), Patterson (1968), Butot & Kiauta (1969), Kiauta & Butot (1969), Vitturi *et al.* (1982), and Ramos & Aparicio (1985). The haploid numbers given in the family and generic diagnoses may be subject to change as further representives of taxa
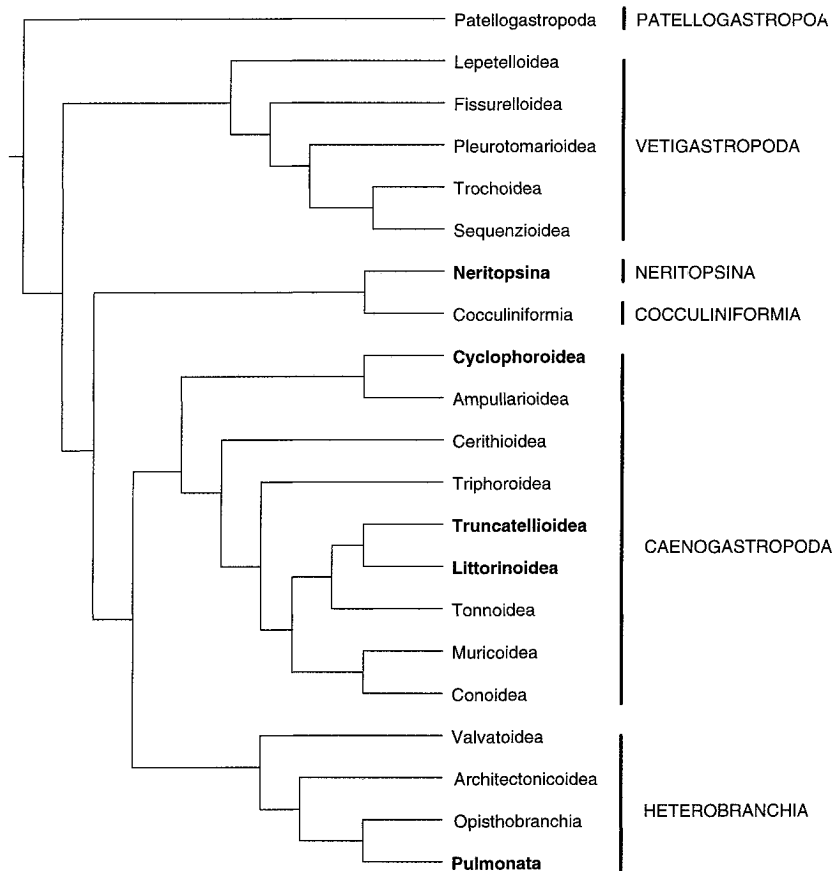
Text-fig. 1 A phylogeny of the mollusc class Gastropoda, adopted from Ponder & Lindenberg (1996), showing distribution of terrestrial lineages (in bold) among the six main subclass taxa recognised (in capitals on right). Extant Cyclophoroidea are all terrestrial, while Neritopsina, Truncatellioidea, Littorinoidea, and Pulmonata are represented by families in marine, freshwater, and terrestrial environments. Stylommatophora represent that dominant terrestrial radiation within the Pulmonata, and worldwide are the dominant group of gastropods on land.

are studied cytologically.

Because of the considerable uncertainty about the phylogenetic robustness of higher taxonomic categories and their respective relationships (see Phylogeny & Systematics), the systematic descriptions in this contribution are arranged in alphabetical order of families.

PHYLOGENY AND SYSTEMATICS

The Mollusca are in appearance, anatomy, ecology, and physiology a highly diverse group, for which the phylogenetic pathways and higher classification have been con-troversial since the very beginning of comparative investigation. Within the Mollusca, most systematic problems arise among the ecologically most disparate Gastropoda. Most gastropods are marine, but several lineages have colonised freshwater and/or terrestrial environments. Worldwide, terrestrial molluscs have been estimated to number about 35 000 extant species (Solem 1984b), and are represented in the gastropod clades Neritopsina, Caenogastropoda, and Heterobranchia (Text-fig. 1). In the heterobranch lineage, Pulmonata have radiated most extensively in terrestrial habitats, and in most regions of the world they dominate the faunas in species richness and
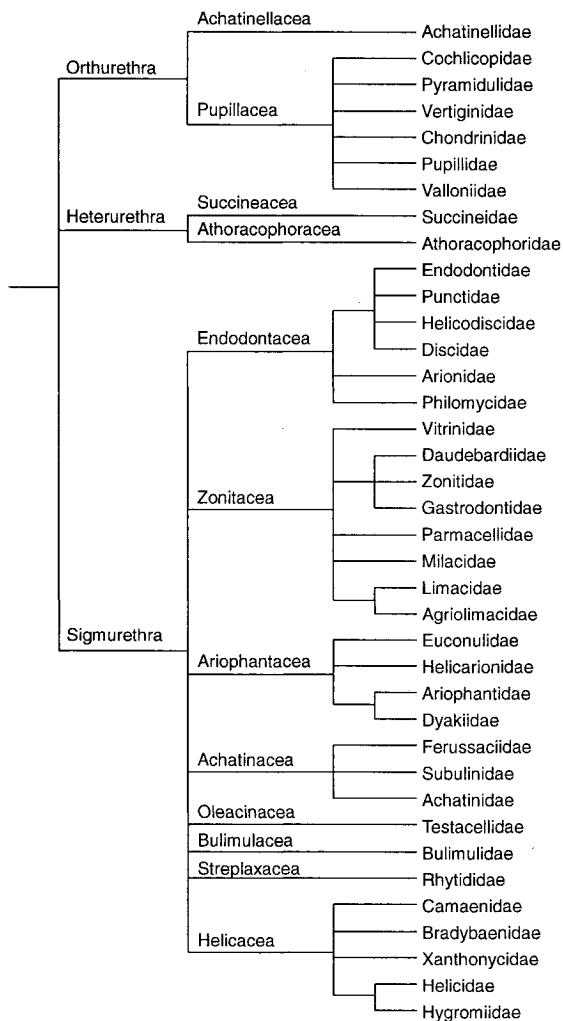
Text-fig. 2 A phylogeny of the Stylommatophora inferred from the classification of Zilch (1959–60).
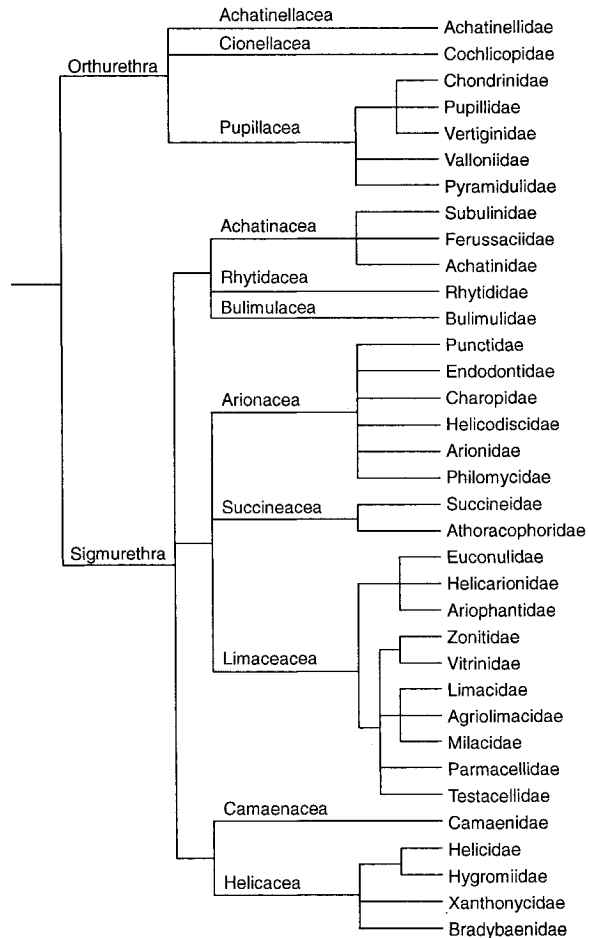
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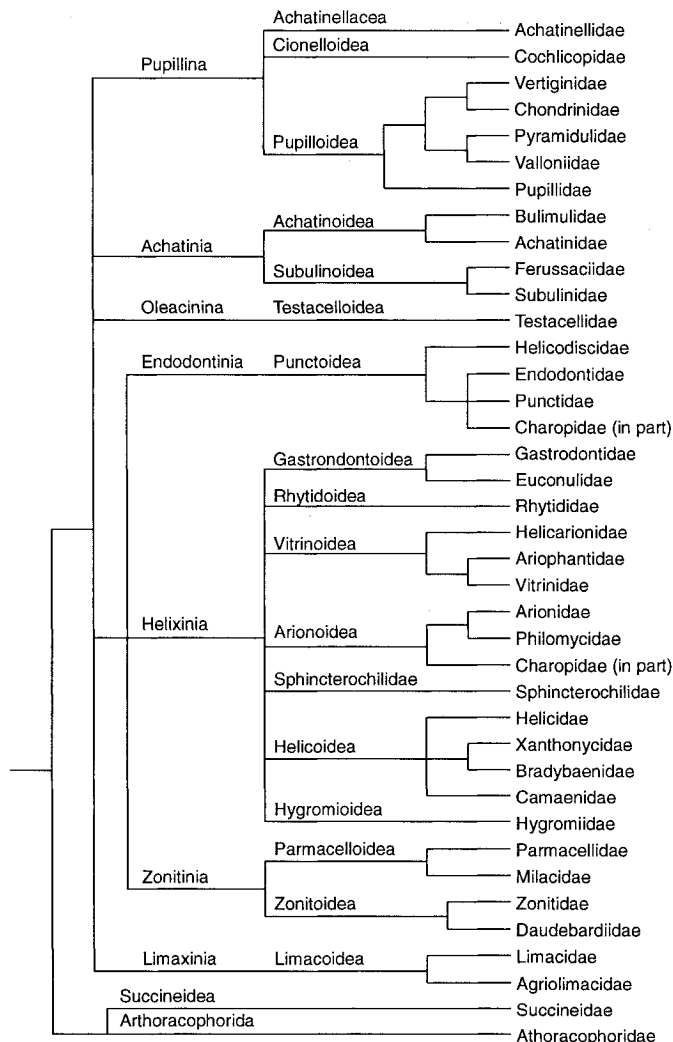
Text-fig. 4 A phylogeny of the Stylommatophora inferred from the classification and cladogram of Schileyko (1979).
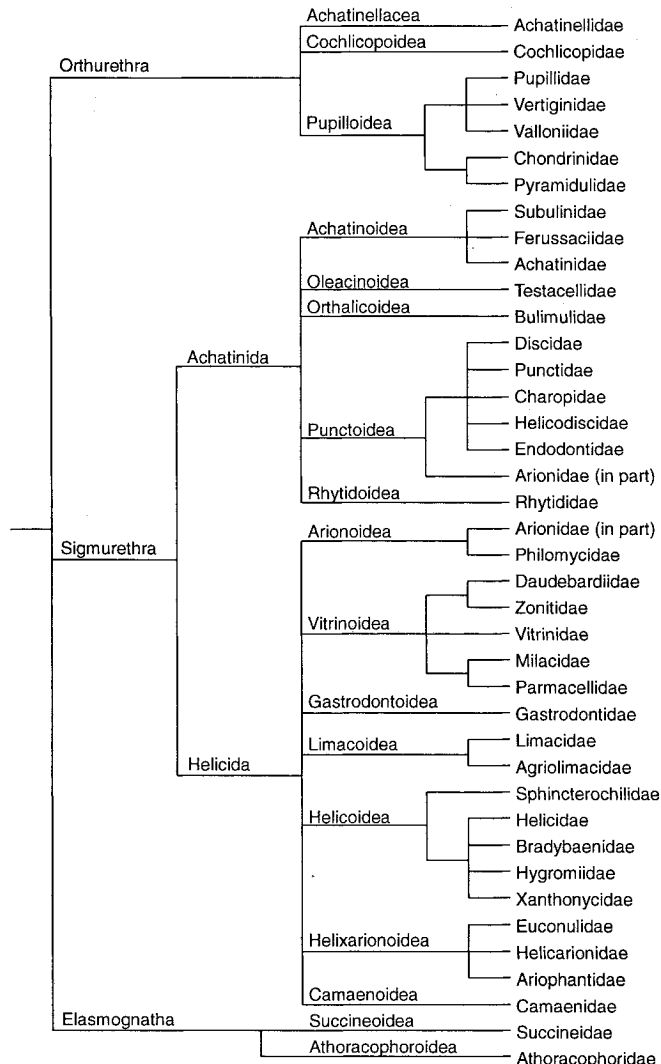
Text-fig. 5 A phylogeny of the Stylommatophora inferred from the classification of Nordsieck (1986a).
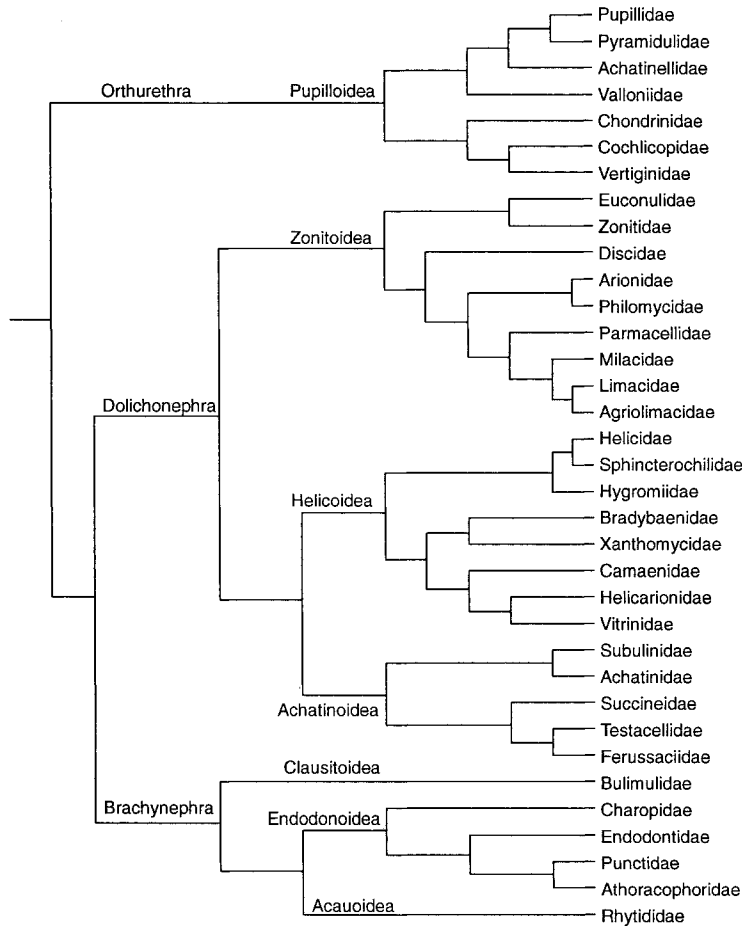
Text-fig. 6 A phylogeny of the Stylommatophora
inferred from the classification and cladogram of Tillier (1989).
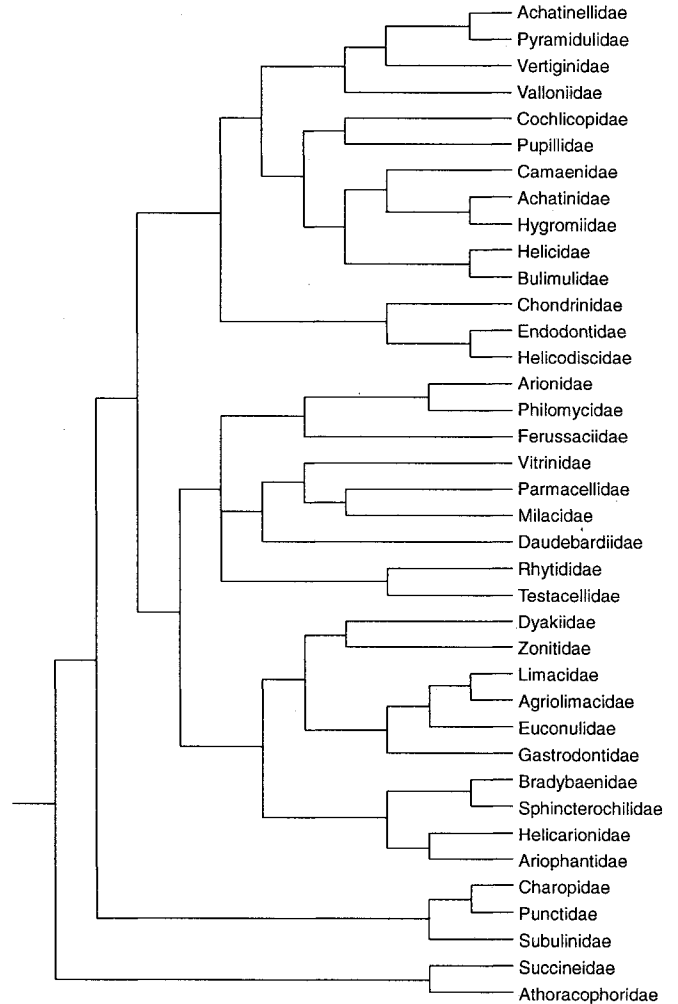
Text-fig. 7 A possible phylogeny within Stylommatophora generated by maximum parsimony analysis of 37 anatomical characters and conforming to a backbone tree suggested by RNA sequence data of Emberton *et al.* (1990) and Tillier *et al.* (1992, 1994). Heuristic search optimisation, with multi-state taxa interpreted as polymorphism. Tree length 1266, Consistency index 0.58.

abundance. Members of the order Stylommatophora are strictly terrestrial, and constitute the dominant group of pulmonate Mollusca on land.

The monophyly of the Pulmonata is generally accepted, with the development of the pneumostome and of a procerebrum combined with a cerebral gland (the latter perhaps homologous to the subtentacular ganglion of the Opisthobranchia) as autapomorphies. However, the phylogenetic relationships of the various adaptive radiations recognisable within Pulmonata have not been fully resolved, and as a consequence taxonomy and nomenclature have been unstable. This has for the most part been due to differing interpretations of pathways of evolutionary change in conchological and anatomical characters (e.g., Pelseneer 1901, Thiele 1929–31, Hubendick 1945, Pilsbry 1948 (1939–48), Morton 1955a, b, Baker 1955, van Mol 1967, 1974, Delhaye & Bouillon 1972a, b, c, Minichev & Starobogatov 1975, Visser 1977, 1981, Tillier 1984a, b, 1989, Haszprunar 1985, Golikov & Starobogatov 1988, Haszprunar & Huber 1990, Nordsieck 1992) and a failure to employ autapomorphies as a basis for taxon definition at all levels of classification.

This problem of unresolved phylogeny and unstable systematics has been particularly acute for Stylommatophora, with high levels of discrepancy at superfamilial level even among classifications proposed over the last two decades (Emberton et al. 1990). According to which of the current schemes is accepted, between 71 and 92 stylommatophoran family-level taxa are recognisable, of which none have been demonstrated by autapomorphies to be monophyletic.

Perhaps the most widely adopted taxonomies for Stylommatophora are those developed by Zilch (1959–60) and Solem (1978). These represent modifications of the scheme developed by H.A. Pilsbry and H.B. Baker, based primarily on excretory, locomotory, and gross reproductive anatomy. Zilch and Solem used an intuitive evolutionary approach, presenting an hierarchically arrayed classification with no formal phylogeny. Schileyko's (1979) approach was similar to that of Zilch and Solem, yet his classification was profoundly different, being based primarily on shell and reproductive morphology. From a reinterpretation of the widely scattered literature on the morphology of the shell and various organ systems, and analysis of geographical distribution, Nordsieck (1985, 1986a) produced the first overtly cladistic stylommatophoran classification. More recently, Tillier (1989) proposed a classification based on cladistic but largely phenetic analysis of new data sets on the anatomy of the digestive, nervous, and excretory systems. Tillier's scheme has been rejected by Nordsieck (1992) and Emberton (in Emberton & Tillier 1995).

The classification schemes for the Stylommatophora by Zilch (1959–60), Solem (1978), Schileyko (1979), Nordsieck (1986a), and Tillier (1989) are illustrated as cladograms in Text-fig. 2–6, with only those families mentioned in the systematic part of this paper identified as terminal taxa. These cladograms were constructed from the hierarchical classification presented by the respective authors. Phylogenetic analyses undertaken by the present author, using maximum parsimony of 37 anatomical characters and constrained to comply with backbones trees suggested by ribosomal RNA sequence data (Emberton et al. 1990, Tillier et al. 1992, 1994), suggest a quite different cladogram topology (Text-fig. 7) and raise serious doubts about the phylogenetic robustness of higher taxon categories in the previously published stylommatophoran taxonomies. The Orthurethra and Sigmurethra, as currently recognised, may not constitute natural phylogenetic groupings.

MORPHOLOGY AND DIAGNOSTIC FEATURES

In this section the morphology of the Stylommatophora is surveyed as a basis for highlighting trends in the evolution of these animals and introducing the characters that have been employed in systematics and taxonomy.

General body plan (Fig. 1–4)

In stylommatophoran land snails one can recognise the conical visceral mass (visceral hump), which is coiled into a spiral within the univalve shell, and the head-foot. The coiling of the visceral mass is generally dextral (clockwise spiral rotation from the embryonic shell down), but is sinistral (anticlockwise) in some species, or even individuals within a species. Any orientation stated or implied below refers to the condition in dextral animals. This coiling results in an asymmetrical body plan. The head-foot is concerned with sensory and locomotor activities, and is protruded from the protective shell during movement and feeding. Head-foot protrusion is mainly effected by hydraulic pressure, but its withdrawal is effected by contraction of muscles connecting the head-foot with the columella, of which the origin is the inner wall of the shell.

The pallial border or mantle collar forms the limit between the head-foot and the visceral mass, and is generally the only part not protected by the shell when the animal is retracted. The ventral surface of the foot is the pedal sole, which is used for crawling by means of ciliary or muscular waves. Locomotion is assisted by a carpet of mucus laid down on the substrate by the suprapedal gland, the opening of which is situated above the anterior extremity of the pedal sole. The part of the head-foot anterior to the pallial border is the cephalic region, or head, which bears the (usually) invaginable ocular peduncles and infer-

ior tentacles. Each ocular peduncle is equipped with an eye at its apex; eye usually pigmented black, but sometimes unpigmented in subterranean forms. The part of the foot posterior to the pallial border is the tail; its posterior extremity sometimes includes a caudal mucous gland.

Two principal cavities in the internal anatomy, the pulmonary cavity and the general body cavity, may be distinguished in land snails. The pulmonary cavity occurs above and behind the head, but within the shell. Its floor, the diaphragm, is formed by the dorsal surface of the head-foot, and its roof by the mantle skirt, a thin fold from the anterior face of the visceral mass. During ontogeny the pulmonary cavity forms by invagination at the border of the mantle skirt, which secondarily fuses with the pallial cavity, which is homologous with the caenogastropod pallial cavity, to form the pneumostome or respiratory orifice (Regondaud 1964, Tillier 1984b).

The pneumostome opens on the right side of the pallial border, in the parieto-palatal angle of the shell aperture. The heart and kidney occupy the proximal part of the pulmonary cavity roof. This whole system of respiratory and excretory organs within the pulmonary cavity is frequently referred to as the pallial complex. For the land snail this cavity not only serves as the site for respiratory and excretory functions but also provides a space that can be occupied by the head-foot when the animal retreats to the protection of the shell.

The larger, general body cavity contains the digestive tract, central nervous system, arterial system, reproductive organs, and free muscle system. This cavity extends forwards into the cephalic region of the head-foot, but in snails does not extend into the tail. Only in the most evolved slugs is the visceral mass housed in a tail cavity (see below). In the snail, those organs that pass from the visceral mass into the head-foot are arranged and structured so as to maintain the pulmonary cavity as a retreat space.

Shell (Fig. 5–9)

The shell gives the mollusc partial or complete shelter for its body, and is composed of several layers: a thin outer organic layer or periostracum, consisting of tanned proteins, overlying much thicker layers of ostracum, which comprises crystalline calcium carbonate and proteinaceous conchiolin. The shell is formed by accretionary growth at the mantle edge. The mantle is a thin membrane which in the active animal extends minutely beyond the shell aperture, and at its edge adds a shell increment to the aperture margin so that each increment copies a configuration of the mantle edge at that time.

The shell tube coils in a logarithmic spiral, retaining isometric proportions between length, area, and volume parameters as it grows. The cross-sectional shape of the shell tube, and the rate at which the tube expands and descends, determine the overall shape of the shell. The inner wall that forms the axis of the shell coiling is referred to as the columella. The whole of ontogeny is conserved in the shell, as the larval shell, or protoconch, is retained as the apex to the post-embryonic shell, or teleoconch. Stylommatophoran snails have limited capacity to alter juvenile parts of their shell by internal resorption and deposition, and, with the exception of a few taxa in which the apical part of the shell may be lost through decollation, the exterior of the shell can not be modified.

The protoconch generally has a clearly defined termination, marking the growth change at the time of hatching from the egg. Usually the protoconch is small and completes a little over one 360-degree rotation or whorl. In some land snails, however, the protoconch may make three to four whorls, and this embryonic growth may account for over one-third of the total shell whorls in mature animals. The surface of both the protoconch and teleoconch is frequently sculptured, and evolutionary changes are often conserved as changes in sculpture running from the teleoconch back onto the protoconch.

Many stylommatophorans exhibit indeterminate growth, whereby the shell continues to grow throughout the life of the animal. Others exhibit determinate growth, whereby increase in shell size is terminated about the time the animal reaches adulthood. In these latter species onset of adulthood is frequently accompanied by changes in the allometric growth of the shell.

The colouring of the shell is produced by organic pigments acquired by the animal from its food. Most of the groups of pigment-producing cells are localised along the margin of the mantle, at the site of shell growth. The resulting colours are the outcome of the combination of four basic types of pigments: yellow carotenoids, black melanins, green porphyrins, and blue or red indigoids. The basic colour and pattern design are determined genetically, although many snails display much variation in colour due to environmental influences.

Because its appearance is characteristic for each species, the shell is very important in molluscan taxonomy, especially in species identification. Many species descriptions have been based soley on the shell. However, many unrelated taxa can through convergent evolution assume very similar shell morphologies. Furthermore, in some lineages there is little specific differentiation in shell characters. In these situations, knowledge of the anatomy of the animal is essential for identification and for resolving relationships.

Terminology for the various components of the shell is illustrated in Fig. 5–7. The shell must be observed in lateral, ventral, and dorsal orientation, and often at vary-

ing magnifications, in order to see all the diagnostic features. The size and general form of the shell are primary in snail identification. Among stylommatophoran snails the shell form varies from elongate to globose, and from depressed to discoidal. This general form can be described in an approximate way by the ratio of height to diameter. The shell may have many or few whorls, which may be rounded, angular, shouldered, or flattened. Generally the viscera fill the shell cavity up to its top and the length of the visceral mass increases with the length of the shell (in whorls). The suture line where one whorl overlays and cements to the preceding one will be impressed to varying degrees, and may be channeled or crenulated.

The growth of the shell as a spiraling tube, with fusion of the inner walls where one spiral or whorl abuts the previous one, creates the axial columella. The columella may be solid, but more frequently comprises a hollow shaft, capped by the protoconch at the apex and open at the shell base. Shells with this hollow columella are generally referred to as perforated, with the hollow axis open to the shell base termed the umbilicus.

The opening of the shell tube is the aperture, and its free margin, minutely covered by the mantle collar in the active animal, is the peristome. The outline of the shell aperture may take many forms owing to the shape of the whorls and their interrelationships. The peristome may be thin and sharp throughout the life of the animal, but in some species with determinate growth the peristome may be variously thickened and/or turned back upon the animal reaching adulthood.

Development of various folds, calluses, tubercles, constrictions, and plates that effectively narrow the shell aperture is a common phenomenon in Stylommatophora. Solem (1972b) referred to these aperture structures as 'barriers'. The general assumption has been that these barriers hinder possible predators from reaching the animal after it has retreated behind the barriers (Guilding 1829, Cooke 1895, Solem 1972b). Suvorov & Schileyko (1991) suggest that the presence of aperture barriers ensures that all soft parts withdraw along constant trajectories, reducing compression damage to organs. They also suggest that the lamellae developed on the columella serve as blocks over which the pedal branches of the columellar muscle are thrown, aiding lift of the shell apex during locomotion (see below for a description of the columellar muscle system).

The number, position, shape, and size of these barriers (Fig. 8, 9) frequently have been used as diagnostic features for both genera and species, especially in families where the shell is rather uniform in appearance. Often these details provide the easiest and quickest means of identifying sympatric congeneric species that are similar in shell shape and size, although intraspecific variation should be recognised. The barriers that occur on the shell axial walls or columella are referred to as columellar lamellae, while those on the parietal wall are known as parietal lamellae. The folds on outer shell walls are referred to as palatal plicae. The palatal plicae result from folding of the secretory surface of the mantle during the life of the animal, but most frequently at the termination of post-embryonic development. In contrast, the columellar lamellae appear even in embryogenesis and continue to lengthen as the shell grows. Frequently, as the barrier is formed at the shell aperture, that part formed earlier and now lying deep within the shell is resorbed.

On the basis of ontogeny, Schileyko (1979) regarded the presence of lamellae as a plesiomorphous character, while the plicae were considered to have evolved independently in several lineages. Nordsieck (1986a) emphasised, however, that irrespective of the ontogeny in extant taxa, the presence of lamellae and plicae must be evaluated as plesiomorphous, because they are found in taxa considered ancestral to the Stylommatophora.

Some species produce shells in which shape does not change with increasing size. However, most exhibit some degree of biphasic or triphasic allometry. The allometric variation often occurs as a slight change in direction of shell coiling at the onset of adulthood. In species with determinate growth, change in shell shape often occurs shortly before secretion of a definitive lip or reflection to the apertural peristome. Shells from adult animals are therefore most useful in identification.

Various sculptural features often occur on the surface of the protoconch and/or the teleoconch. These sculptures may be formed by the calcareous ostracum, overlain and elaborated by the periostracum, or formed solely by outgrowths of the periostracum. Often the sculpture is complex, and its true nature is revealed only at high magnification. The protoconch often becomes eroded during the post-embryonic life of the animal, as may some of the periostracal sculpture of the teleoconch.

Shell loss (limacisation) (Fig. 2, 4)

The term 'slug' refers to a gastropod mollusc with the shell completely lost or so reduced as to be unable to contain the animal. The slug form has evolved many times in gastropods living in marine and terrestrial habitats (a process termed 'limacisation' by Solem 1974), and many taxa of widely divergent origins have, by parallel evolution, assumed a remarkable similarity. They have sacrificed the protection offered by possession of a shell for the mobility, faster body movement, and ability to occupy very small spaces gained by reducing or eliminating the shell. Slugs are simply snails with a reduced shell, and therefore not a

natural group of closely related animals.

In the course of limacisation among Stylommatophora, the number of whorls described by the visceral mass is reduced and its contents are incorporated into the head-foot (van Mol 1970, Solem 1974, Likharev & Wiktor 1979, Tillier 1984a). In semislugs, which represent the intermediate stage in the evolution towards the slug form, the shell is reduced to the extent that the animal can no longer withdraw its head-foot under the protective shell, and the organs associated with the distal part of the visceral mass are incorporated into the anterior head-foot. In these animals the stomach and associated digestive gland remain in the visceral hump, above the pallial border. In full slugs the visceral hump is still more reduced or absent, and the stomach is included in the pedal cavity of the head-foot. The pallial border or mantle collar extends over the surface of the reduced shell and may cover it totally, forming a dorsal mantle shield or 'clypeus'; the shell is absent in some full slugs. In the most limacised slugs, the shield itself can hardly be distinguished from the dorsal surface of the head-foot.

While on a global scale their species number is greatly exceeded by fully shelled taxa, slugs or semislugs are highly diverse, and in many regions make up a significant part of the stylommatophoran fauna. Among the New Zealand indigenous fauna the slug form is represented in the families Athoracophoridae, Rhytididae, and Charopidae. The naturalised Arionidae, Limacidae, Agriolimacidae, and Milacidae are readily distinguished from the native slugs by having no external shell and by carrying dorsally and anteriorly a saddle-shaped mantle shield. The naturalised *Testacella* Draparnaud, 1801 (Testacellidae) shows some similarities with the native rhytidid *Schizoglossa* Hedley, 1892 and the charopid *Flammoconcha* Dell, 1952, but it is distinguished by having the shell at the extreme posterior of the body, the body scored by two branched longitudinal grooves, and the adult being considerably larger.

External pedal and cephalic features
The tegument or skin of the dorsal aspects of the head-foot is typically thick and of rugose, granular pattern. The skin is kept moist by mucus extruded onto the surface from secretory cells dispersed among the epithelial cells. The dorsal aspect of the tail in snails is generally without important features but species in some families (e.g., *Lysinoe* Adams & Adams, 1855 in Helminthoglyptidae, *Oxychona* Mörch, 1852 in Bulimulidae) possess distinct keels. Such keels are even more prominent in slugs of various families, including Milacidae, Limacidae, Agriolimacidae, Parmacellidae, Trigonochlamydidae, and the arionid subfamily Ariopeltinae. A mucus pit, commonly

but wrongly referred to as the caudal mucus gland, is a plesiomorphic character at the posterior extremity of the tail, sometimes with a projection above this juncture. The caudal mucus pit has been lost in many stylommatophoran lineages.

The ciliated ventral surface of the head-foot, the sole, functions as the locomotory pad. It is primitively uniform, although commonly the outer edges are of different colour from the central zone. Locomotion in Stylommatophora is either by pedal cilia or by pedal muscular gliding. Ciliary movement is a smooth, uniform gliding with no differential movement of parts of the sole, propelled by cilia on the sole. This type of locomotion is generally confined among stylommatophorans to small species. Direct monotaxic pedal waves (Miller 1974) are the most common form of locomotion in stylommatophorans, and the only one found in the larger species. This locomotion involves rhythmic pedal waves, initiated at the posterior of the sole and moving to the anterior. In many species the pedal waves extend the full width of the pedal sole. In others the sole is tripartite, with two distinct furrows dividing it into three definite zones, and only the central zone is involved in the locomotory pedal waves. Both ciliary and pedal wave types of locomotory activity are present in lower gastropods (Miller 1974, and references therein). In active stylommatophoran snails the shell may be carried in an elevated position well above both tail and substrate, or in an elevated position but supported by the body whorl resting on the tail, or may rest on the substrate and be dragged in a rhythmic hitching motion.

Two morphological conditions of the foot margin have been recognised in Stylommatophora. In some taxa a pair of grooves – the so-called parapodial grooves – occur along the side of the animal, just above the foot margin, so that the ciliated sole extends above the foot margin. This has been termed the aulacopod condition. In other taxa the holopod condition occurs, whereby the parapodial grooves may be fused into one and are sited at the margin of the foot; or the grooves may be entirely absent, such that the ciliated sole reaches to the lateral margin of the foot (but does not extend above).

Pilsbry (1896) divided the stylommatophoran order Sigmurethra (see below for definition of Sigmurethra and Orthurethra) into two suborders, Aulacopoda and Holopoda, on the basis of whether or not a pair of parapodial grooves occur along the side of the foot. However, Wächtler (1935) showed that the parapodial grooves are not absent from the Holopoda, but are merely indistinct. He showed that these grooves are similarly present but indistinct in various Orthurethra. Webb (1961a) independently repeated Wächtler's discovery of the universality of parapodial grooves, and dismissed the recognition of

ordinal taxa according to distinctiveness of the grooves, on the grounds of ecologically induced convergence. Webb (1961a) thought the aulacopod condition better adapted to burrowing in soil and the holopod condition, with less pronounced grooves, more dry-adapted. Without reference to Wächtler's or Webb's viewpoints, Solem (1978) maintained that the suborders "seemed coherent assemblages" and were thus retained in his sigmurethran classification. Drawing on the comparative morphology of the parapodial grooves throughout the Stylommatophora, Schileyko (1979) maintained that aulacopody arose repeatedly from the holopod condition.

In an analysis of pallial and foot character evolution in Stylommatophora, Baker (1955) concluded that the ancestors of the Sigmurethra probably had, among other features, an aulacopod foot. Tillier (1989) noted the general correlation between an aulacopod foot and a shell with indeterminate growth. With the observation of aulacopody in embryos and hatchlings of Orthurethra and holopod Sigmurethra, Tillier surmised that both the aulacopod foot and indeterminate growth result from paedomorphosis.

The cephalic region is simply an anterior elongation of the head-foot that bears dorsally a pair of ocular peduncles, anteriorly a pair of inferior tentacles or rhinophores, and ventrally a mouth surrounded by oral labels or lobes. The ocular peduncles in Stylommatophora are frequently referred to as tentacles, implying homology with the cephalic tentacles of lower gastropods. Such an homology has not been demonstrated, and the ocular peduncles may have developed from the eye-bearing swellings or short peduncles at the base of the cephalic tentacles seen in some vetigastropods and caenogastropods (Haszprunar 1985). Inferior tentacles are a synapomorphy of the exclusively air-breathing pulmonates (Eupulmonata *sensu* Haszprunar & Huber 1990). These structures have been secondarily lost in some species of the families Urocoptidae, Vertiginidae, Pupillidae, and Succineidae, and in all species of Athoracophoridae.

Respiratory and excretory systems (Fig. 10–14)

In the primitive gastropods, as exemplified by extant Vetigastropoda, the excretory organs were paired and located in the visceral cavity, and respiration was effected by paired ctenidia or gills in the pallial cavity. The pulmonates evolved from gastropods that had lost the ctenidia and which retained only the left excretory organs that became pallial rather than visceral in location. The excretory system of all Stylommatophora essentially consists of a pallial kidney which receives wastes from the pericardium via a nephrostome (renopericardial pore) and expels the excreta through a nephropore (nephridial or ureteric pore) into a ureter, which may be represented by an open

ciliated groove or a closed tube, its length varying among taxa.

I follow Delhaye & Bouillon (1972a, b, c), Nordsieck (1986a, 1992), and Tillier (1989) in recognising the kidney as comprising two morphologically and functionally distinct parts: a broad, proximal, internally lamellate nephridial sac (nephridium) and a distal ureteric pouch (termed 'orthureter' by Nordsieck). The lamellate inner walls of the nephridium resorb ions and water from the waste liquid coming from the pericardium and canalise the residues to the orthureter and ureter.

In snails the kidney, on the left side of the pulmonary cavity roof, is approximately triangular in shape and its base shares a common wall with the visceral cavity, where it runs along the periaortic intestinal bend. The pericardium is applied to its left side and is prolonged towards the pallial border by the pulmonary venous system and towards the visceral cavity, outside the pulmonary cavity, by the aorta, which crosses the intestinal bend before dividing into anterior and posterior branches. Its rectal side parallels the rectum's run along the suture. The ureteric groove or tube runs backwards from the nephropore, which is usually at the recto-pericardial summit of the kidney, along the rectal side of the kidney to the top of the pulmonary cavity, and turns forwards along the rectum to the pneumostome. The ureter is usually considered as comprising two sections: the primary ureter running back along the kidney, and the secondary one running forwards along the rectum to the mantle collar.

The pulmonary vein usually produces extensive vascularisation over much of the pallial surface between the kidney and pneumostome. This is the site of respiratory gas exchange. The contractile pneumostome opens and the diaphragm contracts to dilate the pulmonary cavity and draw air in. Closure of the pneumostome and relaxation of the diaphragm produces a positive pressure inside the cavity, facilitating gaseous exchange across the venous network on the pulmonary cavity roof. The pneumostome again opens to initiate repetition of the cycle.

The higher systematics of the Stylommatophora generally used today originates from Pilsbry (1900), who founded it on the structure of the excretory system. This systematics was rejected by Simroth (1910b) and Thiele (1929–31) as not natural, yet it was developed further by Baker (1955), and after adoption by Solem (1959) and Zilch (1959–60) was generally accepted. Recently this systematics has been called into question again by Schileyko (1976, 1979), Nordsieck (1985), and Tillier (1989).

Pilsbry (1900) proposed the ordinal group Orthurethra for taxa possessing both nephridium and orthureter, but usually with only the proximal part of the ureter developed as a groove. The taxon Mesurethra was defined as pos-

sessing neither an orthureter on the nephridium nor a closed ureter, while Sigmurethra was defined as lacking an orthureter but possessing a ureter running along the anterior of the nephridium to the top of the pulmonary cavity and then, adjacent to the rectum, to the pneumostome. The ordinal category Heterurethra was created by Pilsbry for the Succineidae, the excretory system of which was said to differ from that of the Sigmurethra in that the nephridium extends transversely and the primary and secondary arms of the ureter are at right angles to each other. Baker (1955) applied the term Heterurethra to all stylommatophorans having a transverse nephridium but, as pointed out by Solem (1978) and Nordsieck (1985), this configuration is really a variant of the sigmurethran configuration.

The possession of an orthureter on the distal part of the nephridium is probably plesiomorphic in Stylommatophora because this configuration occurs in basal pulmonate groups (Delhaye & Bouillon 1972a, c, Nordsieck 1985, Tillier 1989). The differentiation of the orthureter in the excretory system among stylommatophorans has generally been recognised only in those taxa traditionally grouped as Orthurethra, namely Pupilloidea, Chondrinoidea, and Partuloidea. Tillier (1989) has demonstrated, however, that a ureteric pouch-like differentiation is present in a number of non-orthurethran families. Despite the homology of these urethric pouch structures not being fully resolved by histological and functional studies, the ordinal status of Orthurethra is called into question. The validity of this ordinal category is further weakened by several orthurethrans possessing a retrograde closed ureter (Watson 1920, Solem 1964, Tillier 1989). Furthermore, many non-orthurethran taxa exhibit transitional states between the ureter morphology used originally to define the Mesurethra and that of Sigmurethra (Nordsieck 1985, Tillier 1989).

Tillier (1989) proposed a new higher classification of non-orthurethrans within the Stylommatophora. Using the differentiation of kidney morphology, he recognised two phylogenetic lines within the Sigmurethra, one in which at first a dedifferentiation of the kidney took place which was followed by a partial closure of the ureter (Brachynephra *sensu* Tillier), and another in which at first a closure of the ureter took place, followed by a partial dedifferentiation of the kidney (Dolichonephra *sensu* Tillier). I concur with Nordsieck (1992) in considering Tillier's hypothesis an overvaluation of the differentiation of the kidney. According to Schileyko (1979) sigmurethry is a feature in embryogensis even in orthurethran forms without a ureter in the adult animal.

Among the marine pulmonates the kidney is differentiated into nephridial and ureteric parts and is without a ureter; this may be the plesiomorphic state in the Stylommatophora. The development of ureters in the terrestrial pulmonates may be correlated with resorption of ions and water. Reduction of the nephridial ureter among Stylommatophora results in an enlargement of the pulmonary cavity respiratory surface.

Reduction in shell size and incorporation of the visceral hump into the head-foot, associated with limacisation, necessarily involve alteration of the layout and size of the pallial organs just described for fully shelled stylommatophorans. Several patterns of pallial organ modification are evident among lineages that evolved towards the slug form. Surface area for gaseous exchange is maintained by the venous vessels being highly developed in the vestigial pulmonary cavity or invading the mantle edge. Most semi-slugs and slugs show extensive development of mantle lobes that partially or wholly cover the shell and/or extend forwards along the neck, providing increased surface area for gaseous exchange (Tillier 1983).

In the most highly evolved slugs a large part of the respiration takes place across the dermis (Duval 1982) and the mantle lobes may be secondarily reduced. Kidney size retention often involves its rotation and change in shape, including the development of lateral lobes. The presence of a closed sigmoid ureter has been considered a prerequisite for evolvement of the slug form (Solem 1974, Tillier 1989), but this paradigm is challenged by the absence of a substantive secondary ureter in testacellid slugs (de Lacaze-Duthiers 1887, this study) and some athoracophorids (G.M. Barker, unpubl. data).

Digestive system (Fig. 15–20)
The digestive system comprises the buccal apparatus, oesophagus, stomach, into which open two lobes of the digestive gland, and intestine (Fig. 15, 16). The spheroidal buccal apparatus, located in the anterior head-foot, comprises a complex arrangement of muscles for protracting and retracting the radula and jaw (Fig. 17, 18). The jaw is located dorso-anteriorly in the buccal cavity, its base firmly anchored in the musculature of the buccal mass wall, and in stylommatophorans is used mainly to hold the food substrate, against which the radula can work.

Primitively the gastropods have two jaw plates, one on either side of the buccal cavity. In several gastropod lineages, including pulmonates, there has been a trend for these lateral plates to be complemented by a series of medially placed plates, which may fuse to produce a single medial plate. In Stylommatophora the lateral elements are absent and the component elements of the medial structure show varying degrees of fusion and variations in overall shape (Fig. 19). The jaw consisting of numerous separate plates united only by a common membrane is termed polyplacognathic. In the stegognathic condition the plates

are soldered together but their edges remain free and usually overlapping. In the aulacognathic condition the plates are completely soldered together and the jaw takes on a vertically striated appearance. In some taxa the jaw plates are completely soldered together but some or all of the plates become enlarged, giving the jaw a ribbed appearance in the condition known as odontognathic. Further reduction in the plates results in an entirely smooth jaw surface in the condition known as oxygnathic.

In all the above, muscle fibres arise from the posterior surface of the jaw and penetrate the buccal musculature. In the elasognathic condition the chitinised plate extends from the posterior of the jaw and is in turn anchored to the buccal musculature. Some early classifications of the Stylommatophora (e.g., Mörch 1865) used the jaw as a diagnostic character, but more recently its variation in size and structure has been considered too great for it to be of value in systematics (Solem 1978).

The radula is a characteristic feature of molluscs. When the animal is not feeding, the radula forms a tongue-like protrusion into the buccal cavity, covered by a radular membrane with few to many thousands of teeth in rows, and is posteriorly prolonged into the radular sac where teeth are formed by specialised cell clusters called odontoblasts. When the animal feeds, the radula is protruded from the mouth, and then withdrawn, to bring the food back into the buccal cavity and oesophagus (Runham 1975). Primarily this buccal system is designed for abrasion, cutting, and ingestion of vegetal matter.

Complex muscles control in and out movement of the radula, during which the radular membrane is rotated partly over the anterior tips of the underlying support of cartilage-like and muscle tissues, known as the odontophore. The rotation of the radular membrane over the anterior face elevates the cutting edge of the teeth above the membrane so that they can scrape, pierce, cut, or tear the object with which they come in contact and produce bits small enough for swallowing.

The pulmonate radula arises in the embryo as two separate areas comprising longitudinal rows of teeth. As the radula develops further tooth rows are added, and the two areas are united as a row of central teeth are added (Kerth 1979a). Thus the primary form of the stylommatophoran radula is a series of transverse tooth rows, and the teeth at the same position on respective transverse rows are essentially mirror images as they are formed by the same odontoblast cells (Kerth & Hänsch 1977, Kerth 1979a, b, 1983a, b, Mackenstedt & Märkel 1987).

Ontogenetic changes in tooth form at a particular position on the radula may continue during post-embryonic life as the odontoblast cells mature or otherwise change. These ontogenetic changes have long been recognised in Stylommatophora (e.g., Sterki 1893b, Quick 1935) but their importance in reducing the reliability of radular differences as a taxonomic tool, or their value in resolving evolutionary trends, has to date received little attention.

Each radular tooth comprises a recurved cutting edge, usually with one or more pointed cusps, supported and affixed to the radular membrane by a basal plate (Fig. 20). The teeth are shaped such that in the elevated feeding mode, each is supported by the basal plate of the tooth immediately adjacent in the same row or in the next anteriad transverse row (Solem 1972a, 1973, 1974). This inter-tooth support system reduces the risk of teeth being torn from the membrane when a hard substrate is contacted. The teeth do, however, become gouged, chipped, or gradually ground down by ongoing abrasion. This wear problem is solved by having new rows of teeth formed at the posterior end of the radula throughout the life of the animal, while at the anterior end the radular membrane is resorbed and the worn teeth are shed to be swallowed and passed out in the faeces. The entire radular membrane with its rows of teeth grows forwards continuously.

The form, size, and number of teeth in each transverse radular row are useful characters in stylommatophoran taxonomy, especially in species identification. Typically, in each transverse row it is possible to recognise a 'central tooth' (also referred to in the malacological literature as the median or rachidian tooth), a series of 'lateral teeth', and a series of 'marginal teeth'. The central tooth is sited in the centre of the radular ribbon on the longitudinal axis, and is usually symmetrical in the shape of its basal plate and cuspid head. On either side, in the same transverse row, the central tooth is flanked by several to many lateral teeth, which may be symmetrical but more typically have the basal plate and cusps most strongly developed on that side of the tooth nearest the radular axis. These teeth in turn are flanked by a series of marginal teeth, which extend to the margins of the radular ribbon. The marginal teeth too may be symmetrical but more often are asymmetrical in shape. In many species the central tooth may be vestigial or even absent.

In taxonomic works the form of the teeth is usually given in the descriptive text, but the structure of the transverse row may be encapsulated in the simple formula
$$N_m + N_l + C + N_l + N_m$$
where N_m and N_l are the number of marginal and lateral teeth on each half row respectively, and C denotes the presence or absence of the central tooth. Thus the formula for a specimen with a central tooth, 6 lateral teeth on either side, and 20 marginal teeth on either side would be
$$20 + 6 + C + 6 + 20$$
If a series of specimens are examined from a single species it is usual to find some variation in numbers of lateral and/

or marginal teeth. In the above example this may be expressed by

$$19–21 + 5–6 + C + 5–6 + 19–21$$

indicating that in the material examined the number of lateral teeth varied from 5 to 6 and the marginal teeth from 19 to 21.

In some species there may be a zone of transition between the lateral and marginal fields in which teeth can not readily be classified as either lateral or marginal. This information can be captured in the formula, and in our example three transitional teeth may be identified by the expansion

$$16–18 + 3 + 5–6 + C + 5–6 + 3 + 16–18$$

In many species the marginal and lateral teeth have assumed the same form. This can be identified in the radular formula as

$$N_{m+l} + C + N_{m+l}$$

where N_{m+l} is the number of teeth in the half row, with no distinction between marginal or lateral teeth.

Evolutionary change in the pattern of cusp and support structure is one of the prime ways in which stylommatophorans specialise to exploit different food resources. Consequently there is a large range in radular tooth form in Stylommatophora. Because of the apparent frequency of diet-related convergence in tooth form, the radula has generally been regarded as useful in systematics only at generic and species level (Solem 1978). Typically there is variation in tooth form and size along each transverse radular row. Furthermore, the transverse row is rarely straight (perpendecular to the longitudinal axis), more typically describing a V or some form of sweeping arc. These variations along the transverse row relate to the complex curvature of the functional face of the radula when the animal is feeding and the differential role in food gathering for teeth at different positions along the row. Evolutionary changes in the dentition generally occur first at the margins of the radula and progressively work their way towards the centre. Independently of such changes, the central tooth may be reduced.

The generalised stylommatophorans feed on decaying vegetation or fungal hyphae and have mostly tricuspid teeth. Typically their radula has 3000 to 4000 teeth. Many groups show specialisations for scraping phylloplane microbes from leaf surfaces and the cusps may become broad and spadelike. Several groups have developed radulae with numerous small multicuspid teeth, as many as 60 000, for raking and piercing algal and fungal cells. Others show a trend towards elongate lateral-marginal teeth on short basal plates, either as multicuspid sweeping structures, or tending to unicuspid, aculeate piercing structures. This elongation of the lateral-marginal teeth is often associated with an overall increase in tooth number to

around 20 000.

Carnivory is generally associated with further development of the aculeate tooth form, so that in the most specialised carnivores all teeth on the radula are lance-shaped for catching and holding prey, and the number of teeth may be reduced to several hundred. Carnivory is usually accompanied by elongation and modified muscularisation of the buccal apparatus, primarily to allow ingestion of large live prey. In its fullest development the buccal apparatus of carnivores occupies a substantial part of the body cavity, and other organ systems are modified to accommodate this. The jaw is commonly reduced or lost in these carnivores, as it plays no role in prey capture.

The oesophagus opens dorsally from the anterior buccal mass and, in snails, runs backwards along the parietal side of the visceral cavity, and most generally expands into a gastric crop a short distance above the top of the pallial complex. Its internal ornamentation, if present, consists of longitudinal ridges. The oesophagus may be partly differentiated into an inflated oesophageal crop but, as pointed out by Tillier (1989), and contrary to the tenets of most treatises of zoology, many stylommatophoran species do not have an oesophageal crop. Two salivary glands are appressed to the oesophagus. Each comprises numerous acini the ducts of which converge into a main salivary duct, and this opens into the buccal cavity at the side of the oesphageal origin. The oesophagus and ducts of the salivary glands pass through the cerebral ring of the central nervous system. The gastric crop is prolonged by the caeca of the gastric pouch or stomach, which collectively extend apically from one-half to two whorls and occupying at least three-quarters of the cross-sectional area of those whorls. At its apex the stomach narrows and abruptly turns forward ventrally as the intestine, which runs along the columellar side of the visceral mass, turns to the left under the anterior gastric crop or the posterior oesophagus, and turns upwards to cross over the aorta clockwise in dorsal view (periaortic bend), describing a posterior loop (prerectal bend) before turning forwards again. The rectum runs along the suture from the summit of the pallial complex to the roof of the pneumostome at the mantle collar. The anterior duct of the digestive gland opens into the concavity of the gastric pouch, between the openings of the stomach and proximal intestine; the posterior duct generally opens through the parietal wall of the stomach. When present, the ventral groove of the gastric crop leads to the opening of the anterior duct, from which one usually short typhlosole emerges into the proximal intestine. A second, longer typhlosole, issuing from the opening of the posterior duct, runs parallel to the first into the proximal intestine and reaches at most the beginning of the periaortic intestinal loop. The typhlosoles are prominent

ciliated ridges that direct food particles and other gastric products into the proximal intestine. The large posterior lobe of the digestive gland occupies most of the space in the upper shell whorls. The anterior lobe, often reduced in size, lies adjacent to the stomach. Structural characteristics of digestive gland cells in Stylommatophora support the view that these cells are responsible for absorption and digestion of food material, as well as production and secretion of digestive enzymes (e.g., Dimitriadis & Hondros 1992).

The digestive tract of the Stylommatophora is rather simplified in comparison with many other gastropods. The oesophagus lacks glandular pouches, and the stomach lacks chitinised gizzard plates or a style sac. The simplification seen in Stylommatophora is correlated with a change from mechanical disintegration of the ingested food to a more chemical (enzymatic) process. In some Stylommatophora, notably the Succineidae and Athoracophoridae, a small caecum or diverticular sac occurs on the columellar side of the stomach near the opening of the anterior digestive gland lobe, and may represent a vestige of the coiled gastric caecum present in many lower gastropod groups. The long intestine is a feature of gastropod herbivores, while shortening of the intestine occurs in carnivorous species in various gastropod groups. Moreover, for stylommatophorans Tillier (1989) found intestinal length to be positively correlated with animal size. Formed faeces are of considerable importance for stylommatophorans because the anus is near the pneumostome, and firm faeces are less likely to foul this. Faeces formation in the distal intestine and rectum generally involves secretion of abundant mucus, squeezing of the mucus and rejected material to form firm bodies, and resorption of water.

The layout of the digestive tract in slugs is somewhat different to that observed in snails, owing to incorporation of the visceral mass into the foot. Tillier (1984a) has described the morphoclines in the digestive tract in the course of limacisation. In most instances and at least in its early stages, limacisation involves dedifferentiation of the gastric pouch and development of a crop. At least in its early stages it also usually involves shortening of the intestine. In advanced slugs lengthening of the intestine may cause either secondary coiling or hypertorsion of the digestive tract, quite independent of the torsion and coiling seen in the ancestral snails, or development of intestinal caeca.

Reproductive system (Fig. 21–23)

Stylommatophora are hermaprodites with a complex reproductive system. Their organs combine female structures associated with production of ova, receipt and storage of allosperm, and production of eggs containing fertilised ova, and male structures associated with production and delivery of autosperm. A generalised stylommatophoran reproductive system is illustrated in Fig. 21, and a generalised layout of the reproductive system in snails and slugs is illustrated in Fig. 22 and 23.

Increasingly, features of the reproductive system are being utilised in stylommatophoran taxonomy and for resolving phylogenetic relationships. However, extensive outgroup comparison is an essential prerequisite for recognising plesiomorphoric conditions and their evolutionary changes in the Stylommatophora.

In the most primitive gastropods the sexes are separate (dioecious), and a single gonad lies near the apex of the visceral hump in the general body cavity. It communicates with the right kidney, the duct of which is therefore a renogenital duct and its aperture a urinogenital pore. At the most primitive level gametes are liberated into the pallial cavity and thence broadcast into the surrounding water, and fertilisation is external. There is therefore generally little or no elaboration of the genital duct or modification for copulation. In some Vetigastropoda, however, the distal portion of the right kidney duct is modified into a glandular region that produces a mucus layer in which eggs are deposited during spawning. The caenogastropods exhibit several developments on this primitive reproductive system.

While hermaphroditism has evolved in some marine caenogastropod families, most – including those families represented in terrestrial habitats – have remained dioecious. The (renogenital) duct from the gonad is separated from the functional kidney to open separately into the pallial cavity. Primitively, the male system comprises the gonoduct elaborated distally into an open ciliated and glandular groove in the pallial cavity, functioning as a prostatic gland, and a muscular phallus on the neck behind the cephalic tentacle. Sperm from the testis (autosperm), mixed with prostatic secretions, is conveyed to the phallus along an open ciliated groove, the sperm groove. In many caenogastropods the prostatic section of the male gonoduct is a closed tube, and the sperm groove has become internalised as a closed duct, the vas deferens. In the primitive caenogastropod female the gonoduct extends along the pallial cavity roof to the right mantle edge. Along its length it is modified into various glandular regions, more or less sequentially continuous, related to provision of nutrients (albumen gland) and protective coatings (capsule gland) in the egg capsules. While primitively this glandular pallial gonoduct is widely open to the pallial cavity, in many taxa the extent of opening has been reduced, with narrow orifices at both proximal and distal ends or, more commonly, just in the distal portion.

At the back of the pallial cavity a seminal receptacle occurs as a simple dilation or a blind diverticulum for storage of allosperm received during copulation (Giusti & Selmi 1985). An additional pouch, the bursa copulatrix or gametolytic gland, connected with the distal pallial gonoduct and opening to the pallial cavity, functions in digestion of spent or excess allosperm. The bursa copulatrix and seminal receptacle are connected by a groove, which Nordsieck (1985) termed the allo-spermiduct.

The gonad of Stylommatophora is formed by one or several clumps of acini which produce both oocytes and spermatozoa and is thus termed ovotestis (or hermaphroditic gland). It is typically embedded in the upper lobe of the digestive gland. From the ovotestis issues a single hermaphrodite duct which conveys both gamete types to the more distal parts of the reproductive system. The hermaphrodite duct is homologous with the gonoduct (renogenital duct) in lower gastropods that primitively conveyed gametes into the pallial cavity. In Stylommatophora the medial part of the hermaphrodite duct is generally dilated, and occasionally structurally elaborated, as a storage site for autosperm (seminal vesicle).

Those sections of the stylommatophoran reproductive system beyond the hermaphrodite duct that function in prostatic secretion, receipt, conduct, and storage of allosperm, and encapsulation of the fertilised ova were derived from – and are therefore homologous with – that section located in the pallial cavity of lower gastropods. Owing to modifications of the pallial cavity, the gonoduct shifted into the body cavity during pulmonate evolution. I shall refer to this section of the stylommatophoran reproductive tract as the pallial gonoduct to reflect this homology.

There has been considerable debate in the literature as to the origins of hermaphroditism and the plesiomorphic state of the pallial gonoducts in the Stylommatophora (e.g., Pelseneer 1896, Simroth 1910a, Hoffmann 1928, Duncan 1960, Nordsieck 1966, 1985, Solem 1972c, 1976, 1978, Visser 1977, 1981, Haszprunar 1985). Monauly of the pallial gonoducts is the plesiomorphic condition in the Stylommatophora (Nordsieck 1985), not diauly as Solem (1976, 1978) believed. Hermaphroditism is a basic feature of gastropods, which is merely suppressed in dioecious taxa. From the condition in the ancestral gastropod, the hermaphroditic pallial gonoduct in the stylommatophoran lineage apparently did not evolve from the female gonoduct or the male gonoduct alone, but arose from the combination of both gonoducts. This hypothesis is supported by the fact that the pallial gonoduct consists primarily of three channels: the outlet-channel for autosperm (termed autospermiduct), the inlet-channel for allosperm (allospermiduct), and the outlet-channel for eggs (oviducal gland).

In most species the pallial gonoducts assume the gross morphology of a sacculate, secretory oviducal gland into which the autospermiduct opens and, with its associated prostatic follicles, is fused. This combined oviducal gland/autospermiduct is commonly referred to as a spermoviduct. The oviducal gland in Stylommatophora retains the function of secretion of mucopolysaccharides and calcareous crystals that form the egg-shell layers. In oviparous species the oviducal gland is commonly elongate and as such the autospermiduct and ribbon of prostatic follicles are similarly elongated. In some oviparous groups there has been some secondary shortening of the oviducal gland or, more frequently, of that section of the autospermiduct from which prostatic follicles issue. In ovoviviparous and viviparous species there is generally a short spermoviduct, with the prostatic follicles confined in reduced numbers at the proximal end. Several groups of stylommatophora exhibit a trend towards separation of the oviducal gland/allospermiduct combination from the autospermiduct, as closed tubes. Diauly of the stylommatophoran pallial gonoducts is therefore interpreted as a secondary phenomenon, and probably has occurred repeatedly.

The seminal receptacle, a diverticulum of the lower gastropod pallial gonoduct that served as a repository of allosperm, has become incorporated into the stylommatophoran reproductive system. Associated with the seminal receptacle is the fecundation pouch, which is the site of fertilisation of ova from the ovotestis. The combined seminal receptacle/fecundation pouch complex is termed the talon. The external form of the talon varies greatly between taxa, from a simple U-shaped bend in the terminal section of the hermaphrodite duct, through to a cluster of minute diverticular sacs, the stem of which arises from the juncture of the hermaphrodite duct with the fertilisation chamber. It lies partially or deeply embedded in the columellar side of the albumen gland.

The plesiomorphic reproductive system of Stylommatophora is equipped with complex copulatory organs, with structures for producing and receiving spermatophores, and an auxilliary stimulatory organ. The free section of the autospermiduct distal to the prostatic follicles and oviducal gland, the vas deferens, is homologous with the structure for conveyance of autosperm evident in lower gastropods. The packaging of spermatozoa for insemination in the form of a spermatophore is of wide occurrence in the Gastropoda. Sperm transfer by spermatophores is neither an adaptation to terrestrial life (Nordsieck 1985) nor a trait developed independently in several stylommatophoran groups (Solem 1978), but a plesiomorphic trait in Stylommatophora inherited from their marine ancestors. In Stylommatophora the spermatophore is produced in the distal part of the vas deferens, which has a special structure

and is termed epiphallus. In the plesiomorphic state the vas deferens does not insert terminally, and therefore the epiphallus has an appendage termed flagellum; this flagellum has a role in spermatophore formation. The shape of the epiphallic organ and its internal folds moulds the spermatophores into species-specific structures.

In many stylommatophoran groups there is an evident trend towards insemination without the need for spermatophores. In its early stages this trend manifests as simplified epiphallic structures, without a flagellum. Further epiphallus simplification results in spermatophores simplified in shape and ornamentation and with reduced thickness of the matrix that ensheaths the spermatozoa. In many Stylommatophora a structure recognisable as an epiphallus is wanting and insemination is achieved by spermatozoa suspended in a viscous fluid. In the plesiomorphic state of the stylommatophoran genitalia the epiphallus opens as a perforated papilla, termed verge, into the tubular phallus. As evidenced by the condition of the structure in Opisthobranchia and Pulmonata, including various Stylommatophora, a long vergic papilla is plesiomorphic for the Stylommatophora. Only rarely in the Stylommatophora is the verge chitinised, and never does it function as a stylet as seen in some Basommatophora and Opisthobranchia. In many Stylommatophora the vergic papilla is reduced in size or entirely absent; this is a secondary phenomenon.

The eversible and thus protrusible phallus in Stylommatophora, developed by invagination of the body wall at the base of the pedal phallic structure, is of widespread occurrence in the lower gastropods, including lower Heterobranchia. This invagination created a tubular structure bearing at its apex the formerly external pedal phallus, as an elongate papilla perforated by the vas deferens or sperm groove – the vergic structure described above. This protrusible phallus, retractable primarily by a muscle attached to the diaphragm or columella, is a synapomorphic character of higher heterobranch gastropods (clade Pentaganglionata *sensu* Haszprunar 1985) but may have developed independently several times with sinking of the pallial gonoduct into the haemocoel.

As exemplified by variations in contemporary archeopulmonate Ellobiidae (Morton 1955a, b, Berry *et al.* 1967), the phallic portion of the vas deferens in early Stylommatophora shifted from a course through the phallus wall to one in the haemocoel, but closely bound to the phallus by a muscular sheath. In contemporary Stylommatophora the vas deferens, or its epiphallic terminal section, has retained this association with the phallic sheath in some taxa while in others it has been lost and in yet others the sheath itself has been lost.

The phallus retractor muscle relaxes during mating to allow the phallus to evert. When copulation is completed,

the muscle – which now lies inside the everted phallus – contracts. This invaginates the phallus as it is pulled back into the body.

Sinking of the pallial gonoduct into the haemocoel has been accompanied in Stylommatophora by a shift forwards of the female opening to unite with that of the male part as a common chamber, termed the atrium. The female component of the genitalia thus comprises a tubular extension of the pallial gonoduct. In Stylommatophora the bursa copulatrix has maintained both its association with the the pallial cavity and its opening to the pallial gonoduct. Thus the primary form in Stylommatophora is a reservoir lying adjacent to the pericardium and bound by connective tissue and muscle to the diaphragm that constitutes the floor of the pulmonary cavity, and a distinct, usually rather long duct running to the cephalopodial part of the female reproductive tract. In many Stylommatophora the bursa copulatrix has developed an even more anterior entry to the reproductive tract, in some taxa communicating directly to the atrium or even with the phallus. A variant of this pattern is the opening of the bursa copulatrix to the proximal region of the female pallial gonoduct in some Achatinellidae.

Two basic types of bursa copulatrix are evident in Stylommatophora, those with a diverticulum on the duct, and those without such a diverticulum. The diverticulum on the bursa copulatrix is widespread in the Stylommatophora, and is apparently plesiomorphic. It is specifically constructed and positioned, relative to the bursa copulatrix duct opening, to function during mating as the site of spermatophore receipt from the copulatory partner. In many taxa the diverticulum is reduced or absent and the bursa copulatrix duct assumes the role of spermatophore receipt. The function of spermatophore receipt and the occurrence of allosperm in the reservoir part has led to the term bursa copulatrix being applied to this structure. However, a gametolytic rather than storage function has been demonstrated for this structure (Tompa 1984).

Furthermore, in many Stylommatophora spermatophores – or seminal mass, where spermatophores are not produced – are not received directly into the bursa copulatrix duct or its diverticulum, but are deposited in the oviduct. The seminal receptacle in the talon is the site for storage of allosperm, and it is only the excess allosperm that are retained or conveyed into the bursa copulatrix for lysis and resorption. Thus the term bursa copulatrix is not entirely appropriate, but is retained here for consistency with the modern literature. A trend evident in Stylommatophora, apparently related neither to site of entry to the reproductive tract nor to body cavity space alterations, is shortening of the bursa copulatrix duct and relaxation of the association of its reservoir with the pallial region.

The free oviduct is its narrower portion, between the distal end of the oviducal gland and the entrance of the bursa copulatrix duct. The vagina is that region of the oviduct between the base of the bursa copulatrix duct and that of the phallus.

Stimulatory organs can be found in the terminal genitalia of many Stylommatophora. There are different opinions concerning their evolution: some authors – Solem (1978) and Tompa (1984), for example – thought the stimulatory organs had evolved independently, while von Ihering (1892) and Schileyko (1979) considered all or only part of them to be homologous.

The stimulatory organ of the Orthurethra (*sensu* Pilsbry), developed as an phallic appendage, consists of a perforated papilla in a sheath, an adjoining gland, and a retractor muscle which is a branch of the phallic retractor. In many orthurethrans the bifid retractor is retained despite the stimulatory organ being somewhat reduced. In other orthurethran taxa the retractor to the stimulatory organ is retained but has become separated from the phallic retractor. A branch of the phallic retractor muscle inserting on the vestiges of the phallic stimulator, represented by a small lateral phallic caecum in Clausiliidae, Zonitidae, Euconulidae, and Ferussaciidae, testifies to the former wide occurrence of a more fully developed stimulatory organ in the non-orthurethran Stylommatophora.

In at least one group of non-orthurethran Stylommatophora, the zonitoid Gastrodontinae, a stimulatory organ of very similar structure to that in Orthurethra, and supplied with a retractor muscle, is present as an appendix to the phallus. It contains, however, a well developed calcareous dart. In Sagdidae too the stimulatory organ on the phallus is remarkably like that seen in Orthurethra, except for the absence of a retractor muscle and the presence of a vestigial dart. In several families of non-orthurethran Stylommatophora (e.g., Ariophantidae, Urocyclidae, Vitrinidae) this dart-bearing stimulatory organ has been retained, but displaced to the atrium or vagina, and the retractor muscle is still evident.

There is little doubt as to the homology of the unarmed stimulatory organ characteristic of the Orthurethra and the dart-equipped organs of these latter Stylommatophora. The difficulty lies in deciding which is the more plesiomorphic. The occurrence of a dart in the stimulatory organ across many superfamilies of non-orthurethran Stylommatophora (the occurrence in Orthurethra has yet to be confirmed – see Tompa 1984), including the vestigial dart of Sagdidae in a stimulatory organ built like the orthurethran stimulator, suggests that the dart-bearing structure is the primitive feature of Stylommatophora. This interpretation of plesiomorphy is further supported by the occurrence of auxiliary copulatory organs associated with the phallus in many other Heterobranchia, e.g., Cephalaspidea and other opisthobranchs, Siphonariidae, Amphibolidae, Ancylidae, Onchidiidae, Vaginulidae, and Rathouisiidae. Nordsieck (1985, 1992) reached the same conclusion.

The reproductive system of Stylommatophora is syntrematic, with the common genital orifice opening on the right side. Syntremy permitted the change in position of the stimulatory organ from the male terminal genitalia to the female ones. Thus, among non-orthurethran Stylommatophora the stimulatory organ may be inserted on the phallus – the plesiomorphic position – or on the genital atrium and vagina. Further, loss of the stimulatory organ is widespread in the Stylommatophora. During evolutionary degeneration of the stimulatory organ, dart loss is a stage that precedes full organ loss; this pathway is evident, for example, in helicoid snails. In many taxa dart loss is accompanied by modification of the previously dart-bearing papilla into a fleshy or hard-coated sarcobelum. Dart loss and stimulator loss are to be regarded as irreversible.

The plesiomorphic state within the Stylommatophora is for the genital opening to be located in the main body of the visceral stalk, near the pneumostome. In many lineages there has been a foward shift of the genital opening, into the cephalic region, and in many taxa the opening occurs immediately behind the right ocular peduncle.

External sperm exchange, by which allosperm is deposited on the mate's everted phallus without intromission, has evolved at least five times among stylommatophorans (Emberton 1994b). In the families Succineidae, Endodontidae, and Polygyridae both internal and external sperm exchange are known, while in Limacidae and Agriolimacidae exchange is exclusively external.

While the hermaphroditic reproductive systems of stylommatophorans typically possess both male and female genitalia (euphally), aphallic individuals that lack the male copulatory organs are known from several families, including Vertiginidae, Valloniidae, Chondrinidae, and Agriolimacidae. Aphallic individuals can self-fertilise, or can outcross as female but not as male.

Tompa (1976, 1980) considered the provision of the embryo with calcium, by ionic mobilisation of shell and/or digestive gland calcium stores and deposition as an egg shell by a specialised gonoduct epithelium, to be a synapomorphy of Stylommatophora. Other gastropods, especially in terrestrial habitats, are known to provide the embryo with calcium in the egg capsule, but the mechanisms for this differ from that in Stylommatophora (Tompa 1980). A hard, calcite egg shell thus can be taken as plesiomorphic in Stylommatophora, and the production of eggs with diminished calcium provision, and hence lacking a shell as apomorphic. Some stylommatophorans

have adopted embryo brooding, whereby the eggs are deposited at an advanced stage of embryo development or retained in the oviduct until hatching (Tompa 1984).

Free muscle system (Fig. 22, 23)

The free retractor muscular system comprises branches of the columellar retractor, which is inserted on the inner shell surface along the columella – the only point at which the animal is attacted to its shell. The primary form of the columellar muscle is a single stem with a broad fan attaching to the pedal musculature and organs in the body anterior. This condition is now rarely seen in the Stylommatophora. Instead there has been a general reduction in the bulk of the free muscle system, with branches to the various anterior organs and cephalic body walls becoming to various degrees separated from the columellar muscle stem. The buccal retractor inserts under the buccal mass, while the tentacular retractors divide distally into ocular and rhinophoral branches. In the primary state, the right ocular retractor passes over the base of the phallus to reach the ocular peduncle. The alternative course of the retractor, free of the terminal genitalia, has apparently arisen in many lineages independently. During limacisation the columellar stem to the pedal musculature is frequently lost, since there is no need for withdrawal of the anterior head-foot. In many slug taxa the buccal and tentacular retractors frequently lose their association with the columella (or its region of origin) and instead arise from the body wall.

As indicated above, the phallus retractor muscle in most Stylommatophora arises from either the diaphragm or the columellar muscle stem. In some taxa the phallus retractor arises from the body wall outside the pallial region. In yet others the retractor is represented by rather weak muscle strands to the pallial gonoduct, or is entirely absent. The plesiomorphic state for attachment of the phallus retractor and the evolutionary changes within the Stylommatophora have not been resolved.

Nervous system (Fig. 24)

In the primitive gastropod the nerve centres are concentrated in the anterior head-foot, forming a loose ring around the oesophagus. There are three pairs of ganglia. The cerebral ganglia, linked by a cerebral commissure, are placed far forward dorsally over the buccal apparatus. Each cerebral ganglion sends ventrally two connectives, one each to the pleural and pedal ganglia located ventrally at the level of the anterior border of the foot. The left and right pleural ganglia are linked to the respective left and right pedal ganglia by a short connective. The pedal ganglia comprise long cords running the length of the foot and linked by many commissures. This arrangement, with the pleural ganglia sited closer to the pedal ganglia than to

the cerebral ganglia, is termed hypoathroidy.

Paired visceral ganglia lie at the base of the visceral mass, linked to the pleural ganglia by connectives which traverse the neck and so are affected by torsion. In consequence the half-loop starting at the right pleural ganglion crosses over the oesophagus to the visceral ganglion on the left, and the half-loop starting at the left pleural ganglion passes under the oesophagus to the visceral ganglion on the right, so giving the crossed condition of the visceral loop known as streptoneury. The dorsal pleural-visceral connective carries medially a ganglion (supraoesophageal) which innervates the left pallial gill (ctenidium) and sensory organ (osphradium). The ventral connective carries a corresponding suboesophageal ganglion, innervating the same organs on the right.

The Stylommatophora are derived from gastropods in which the pedal ganglia had been concentrated and linked by a reduced number (two) of commissures, and the visceral loop had been shortened so that the pleural-visceral connectives were no longer crossed. This condition of the uncrossed visceral loop, referred to as euthyneury, had been accorded systematic significance in uniting opisthobranchs and pulmonates in the clade Euthyneura (Spengel 1881). However, the euthyneurous state of the visceral loop in pulmonates and opisthobranchs is now recognised as being due to convergence and derived independently in different lineages (Haszprunar 1985). Furthermore, vestiges of streptoneury are evident in several extant lower Pulmonata (e.g., Chilinidae, Ellobiidae) and Opisthobranchia (e.g., Diaphanidae, Philinidae). The opisthobranchs and pulmonates are, however, united by the autapomorphy of two additional ganglia – left and right parietal ganglia, derived from left and right pleural ganglia respectively – on the visceral loop. For this group Haszprunar (1985) proposed the taxon Pentaganglionata.

In Stylommatophora, with shortening of the connectives in the visceral loop, the oesophageal ganglia have been merged with the visceral ganglion, and the parietal ganglia frequently become appressed to or fused with the pleural or visceral ganglia. It seems reasonable that the length of the connectives in the visceral loop would be evolutionarily plastic (Tillier 1989); however, once two ganglia fuse in the course of evolution they are highly unlikely to separate again (but see Emberton 1991). The importance of visceral loop configuration for stylommatophoran systematics was initially investigated by Bargmann (1930), recommended by Bishop (1978), and extensively exploited by Tillier (1989) and Emberton (1991). In the present work I have incorporated the configuration of the visceral loop into the taxon diagnoses.

The stylommatophoran central nervous system is sited at the posterior of the buccal mass. The oesophagus passes

below the cerebral commissure but above the visceral loop. For a visceral loop of a given length, the diameter of the perioesophageal ring is smaller when the cerebropleural connectives are shorter than the pleuropedal connectives, in contrast to when the pleural ganglia are closer to the pedal ganglia. Tillier (1989) reasoned that a short visceral loop is in general functionally impossible unless the pleural ganglia are close to the pedal ganglia, because it would strangle the oesophagus.

An extension of his argument would suggest that the hypoathroid condition in Stylommatophora, where the pleuropedal connectives are shorter than the cerebropedal ones, is a secondary phenomenon affected by functionality of the digestive tract. However, the condition in many basal groups indicates that hypoathroidy is plesiomorphic in Gastropoda (Haszprunar 1993). Furthermore, hypoathroidy is retained or achieved in several heterobranchia, e.g., Aplysiomorpha, Ellobioidea, and Trimusculoidea (Haszprunar & Huber 1990), irrespective of the degree of shortening of the visceral loop. Moreover, many Caenogastropoda and other non-stylommatophoran Heterobranchia have achieved epiathroidy, whereby the pleuropedal connectives are longer than the cerebropedal ones, despite in many instances having a shortened visceral loop. On the basis of ontogeny, Haszprunar (1993) thought hypoathroidy in heterobranchs to be derived secondarily from the epiathroid condition.

Long cerebropedal connectives are correlated with a long supraoesophageal cerebral commissure, and this association is probably the plesiomorphic condition (Tillier 1989). A compact nerve ring with short cerebropedal connectives is a common feature in Stylommatophora, and the lengths of the right and left cerebropedal connectives are frequently subequal. In carnivorous taxa the retention or secondary derivation of a long anterior nerve ring, including a rather long visceral loop, can be explained easily by the functional necessity for extending around the voluminous buccal mass associated with carnivory.

The cerebral ganglia are also linked by a thin and easily overlooked sub-oesophageal cerebral commissure. The cerebrobuccal connectives pass from the lower surface of the cerebral ganglia to the buccal ganglia, which are appressed to the buccal mass on either side and below the origin of the oesophagus.

An essential autapomorphy of the pulmonates is the development of a neurosecretory procerebrum – an accessory lobe linked by two connectives to the metacerebral part of the cerebral ganglion – and a cerebral gland. Van Mol (1967, 1974) described morphoclines in the microscopic structure of the pulmonate cerebral ganglia, emphasing greatest systematic significance in the degree to which the procerebrum is integrated with the metacerebrum (persistence of two procerebral commissures) and the position of the origin of the peritentacular nerve. As pointed out by Solem (1985) and Tillier (1989), the conclusions of van Mol cannot be accepted because observations in a single species cannot be generalised to family or even suprafamily levels. Nonetheless, the Stylommatophora can be characterised by an enlarged procerebrum that is extensively fused with the cerebral ganglion.

The cerebral ganglia receive tactile and olfactory sensory input from tentacles on the head and from the lips around the mouth, and visual signals from the eyes; there is a single nerve to each ocular peduncle and to each inferior tentacle. The cerebral ganglia also innervate the buccal muscles. The pedal ganglia mediate locomotor movements of the foot. The pleural ganglia innervate the mantle edge, and the visceral ganglia the organs of the visceral mass.

COLLECTING, PREPARATION, AND CURATION

Empty shells are best stored dry in boxes (large specimens) or gelatin capsules (small specimens). Long-term storage in glass vials is often associated with deterioration of the shell. Field-collected live specimens are best killed by immersion for about 15 hours in de-aerated or narcotised water before preservation in 75% ethanol.

Snails may be extracted from the shell and stored in alcohol for subsequent anatomical examination. This extraction is most readily achieved, without destruction of the shell, if undertaken several hours after placement in the preservative but before the soft tissues have hardened substantially. For large animals preservation of the internal tissues is often improved by making an incision in the body wall to allow rapid penetration of the preservative. Mollusc shells deteriorate in formalin solutions, and formalin should be reserved for fixation and preservation of animal tissues to be used in histological investigations.

Specimens may be dissected under water or 75% ethanol, pinned to black wax in a shallow tray. Visibility of minute structures may be enhanced by addition to the dissection of small quantities of dye solution, such as methylene blue.

Jaws and radulae are extracted from the buccal mass by dissolution of the tissues in 10% sodium hydroxide solution and repeated washing in tap water. For light microscropy these structures can be mounted temporarily on glass slides in glycerol or permanently in Clearmount or DPX. For electron microscopy the jaws and radulae are best brought to 100% methanol and then air dried before being mounted on specimen stubs.

For many species inspection of the protoconch and teleoconch sculpture at high magnification is required. For minute species this is best achieved by scanning electron microscopy. The specimens are first cleaned of most dirt and incrustations by soaking overnight in water, and then immersed for a few seconds in the water-filled tank of an ultrasonic cleaner. After air drying the specimens are mounted with the desired orientation on stubs.

DESCRIPTIONS

Family AGRIOLIMACIDAE

Diagnosis. Small to medium-sized aulacopod slugs, herbivorous or facultatively carnivorous, with a rudimentary internal shell always present. Mantle a large, elongate-oval shield situated in anterior part of body, covering more than 0.3 of body. Posterior of body with a short keel. Pneumostome in right margin of mantle, usually in posterior part. Sole divided into 2 lateral zones with transverse grooves and a central zone with V-shaped grooves. Suprapedal gland embedded in foot tissues. Kidney broadly oval, often with a posterior lobe extending under rectum, partially enclosing heart at its anterior end. Secondary ureter separating from posterior end of kidney, terminating in urinary bladder. Buccal mass spheroidal. Jaw oxygnathic. Radula with marginal teeth dagger-like or sword-like. Intestine with a single forward-directed loop. Cephalic retractors arising near body midline, a little posterior to pallial complex. Right ocular retractor muscle crossing the phallus or free of genitalia. Genital orifice immediately behind right ocular peduncle, or about 0.3 posteriad between peduncle and pneumostome. Oviduct and atrium without accessory glands. Phallus sarcobelum (stimulator) often present. Epiphallus absent; spermatophores not produced. Central nervous system with cerebropedal connectives equal in length, short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact. Haploid chromosome number 30.

Remarks. The family Agriolimacidae has recently been reinstated (Wiktor & Likharev 1979, 1980, Likharev & Wiktor 1980) after having long been grouped with the Limacidae. This taxon comprises over 150 species, most confined naturally to the Holarctic region. Genera included are *Deroceras* Rafinesque Schmaltz, 1820, *Krynickillus* de Kaleniczenko, 1851, *Lytopelte* Boettger, 1886, *Mesolimax* Pollonera, 1888, *Toxolimax* Simroth, 1899, *Megalopelte* Lindholm, 1914, and *Furcopenis* Castillejo & Wiktor, 1983.

Genus *Deroceras* Rafinesque Schmaltz

Limax of authors. (Not *Limax* of Linnaeus, 1758, type species *Limax maximus* Linnaeus, 1758, by original designation; Limacidae.)

Limacella of authors. (Not *Limacella* of Brard, 1815, type species *Limacella parma* Brard, 1815 = *Limax maximus* Linnaeus, 1758, designated by Turton (1831) – synonym of *Limax* Linnaeus, 1758; Limacidae. Not of de Blainville, 1817, type species *Limacellus lactescens* de Blainville, 1817 = *Limax carolinianus* Bosc, 1802, by monotypy – synonym of *Philomycus* Rafinesque Schmalz, 1820; Philomycidae).

Deroceras Rafinesque Schmaltz, 1820: 10, type species *Limax gracilis* Rafinesque Schmaltz, 1820 = *Limax laevis* Müller, 1774, by original designation.

Krynickillus of authors. (Not *Krynickillus* of de Kaleniczenko, 1851, type species *Krynickillus melanocephalus* Kaleniczenko, 1851, by monotypy; Agriolimacidae.)

Megapelta Mörch, 1857a: 282, type species *Limax semitectus* Mörch, 1857a = *Limax laevis* Müller, 1774, by monotypy.

Agriolimax Mörch, 1865: 378, type species *Limax agrestis* Linnaeus, 1758, designated by Malm (1868).

Malacolimax of authors. (Not *Malacolimax* of Malm, 1868, type species *Limax tenellus* Müller, 1774, according to Hesse (1926); Limacidae.)

Krynichia Hazay, 1881: 31, type species *Limax brunneus* Draparnaud, 1801 = *Limax laevis* Müller, 1774, by monotypy.

Diagnosis. Shell a broadly oval internal plate with concentric growth lines radiating from vestigial protoconch at posterior left margin. Keel on body very short. Pneumostome in posterior right margin of mantle. Mantle shield with concentric ridges, their nucleus to right of midline, over respiratory orifice. Kidney oval, with posterior lobe directed to right under rectum. Jaw oxygnathic, with a central protuberance. Right ocular retractor muscle passing to left of phallus and oviduct. Phallus with an internal stimulator and frequently with appendages. Genital orifice immediately behind right ocular peduncle. Rectal caecum often present, short.

Remarks. Until very recently in European and some American literature the name *Agriolimax* Mörch, 1865 was used for all representatives of this genus. I have followed Wiktor (1973) in giving priority to *Deroceras* Rafinesque Schmaltz, 1820.

Deroceras is represented by about 100 species in four subgenera, for which de Winter (1985) provides a summary of the diagnostic characters.

The genus is Holarctic in distribution, with greatest representation in Europe. Several species have been widely dispersed through human activities. Represented in New Zealand by three naturalised species.

Subgenus *Deroceras* Rafinesque Schmaltz

Deroceras Rafinesque Schmaltz, 1820: 10, type species *Limax gracilis* Rafinesque Schmaltz, 1820 = *Limax laeve* Müller, 1774, by original designation.

Malino Gray, 1855: 178, type species *Limax lombricoides* Morelet, 1845, by original designation.

Hydrolimax Malm, 1868: 79, type species *Limax laeve* Müller, 1774, according to Hesse (1926). (Not *Hydrolimax* Heldeman, 1842; Vermes.)

Eulimax of authors. (Not *Eulimax* of Boettger, 1881, type species *Milax brandti* von Martens, 1880, by monotypy; Limacidae.)

Arctolimax Westerlund, 1894 (1892–94): 163, type species *Limax hyperboreus* Westerlund, 1876 = *Limax laevis* Müller, 1774, according to Pilsbry, 1948 (1939–48).

Diagnosis. Body narrow, with sides more or less parallel. Mantle large, almost 0.5 of body length. Skin soft, partly transparent, so shape of internal organs visible. Phallus with anterior part a stimulator in the shape of a hemispherical papilla or obtuse cone; posterior part with 1 or 2 appendices and with glandular papillae or flagella. Rectal caecum absent, or in the form of a small, shallow pocket.

Remarks. Slugs favouring high humidity, living near water in both open and forested habitats.

Deroceras (Deroceras) laeve (Müller)

Figures 25, 28, 68, 109, 138, 165, 191, 219, C1, M32–34; Map 1

agrestis of authors (not of Linnaeus, 1758).
laevis Müller, 1774: 1 (*Limax*).
brunneus Draparnaud, 1801: 104 (*Limax*).
gracilis Rafinesque Schmaltz, 1820: 10 (*Limax*).
andecola d'Orbigny, 1837 (1834–47): 222 (*Limax*).
campestris Binney, 1843: 52 (*Limax*).
parvulus Normand, 1852: 8 (*Limax*).
semitectus Mörch, 1857a: 281 (*Limax*).
valdivianus Philippi, 1858: 22 (*Limax*).
weinlandi Heynemann, 1862: 212 (*Limax*).
araneus Gassies, 1867: 117 (*Limax*).
americana Tate, 1870: 154 (*Krynickia*).
guatemalensis Crosse & Fischer, 1870: 297 (*Limax*).
mouensis Gassies, 1871: 14 (*Limax*).
rarotonganus Heynemann, 1871: 43 (*Limax*).
occidentalis Cooper, 1872: 146 (as var. of *campestris* Binney) (*Limax (Eulimax)*).
brasiliensis Semper, 1873: 84 (*Limax (Malacolimax ?)*).
argentinus Strebel & Pfeffer, 1874: 6 (*Limax*).
montanus Ingersoll, 1875: 130 (not of Leydig, 1871) (*Limax*).
castaneus Ingersoll, 1875: 131 (*Limax*).
ingersolli Binney, 1875: 176 (*Limax*).
hyperboreus Westerlund, 1877: 21 (not of Simroth, 1901) (*Limax*).

stenurus Strebel & Pfeffer, 1880: 21 (*Limax*).
berendti Strebel & Pfeffer, 1880: 22 (*Limax*).
mentonicus Nevill, 1880: 103 (*Krynickillus*).
jalapensis Strebel & Pfeffer, 1880: 22 (*Limax*).
hemphilli Binney, 1890: 205 (*Limax*).
pictus Binney, 1892: 166 (as variety of *hemphilli* Binney) (*Limax*).
zonatipes Cockerell, 1892: 72 (as var. of *campestris* Binney) (*Agriolimax*).
bevenoti Collinge, 1897b: 295 (*Agriolimax*).
ashmuni Pilsbry & Ferriss, 1909: 512 (as subsp. of *hemphilli* Binney) (*Agriolimax*).
pseudodioicus Velichkovskij, 1910: 64 (*Agriolimax*).
motaguensis Cockerell, 1914: 57 (as subsp. of *guatemalensis* Crosse & Fischer) (*Agriolimax*).
renschi Wagner, 1934: 89 (*Agriolimax*).
schulzi Tzvetkov, 1940: 388 (*Agriolimax*).
hesperium Pilsbry, 1944: 16 (*Deroceras*).
monentolophus Pilsbry, 1944: 16 (*Deroceras*).

Slugs (Fig. 25) up to 25 mm in length, usually smaller, slim, posteriorly obtusely narrowing; keel short, ill defined. Mantle shield about 0.5 of body length. Body wall thin, transparent, usually chocolate brown, grey, or black, less frequently brownish cream, unicolorous in apparence but under magnification seen to be speckled or flecked. Border of pneumostome rather inconspicuous. Sole pale grey to brown, more transparent medially than laterally. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 28) thin, white, oblong-oval to ovoid with right margin straight to convex, up to 3.1 x 2.1 mm. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, non-protruding, situated asymmetrically at left side. An organic sheet surrounding shell.

Reproductive system, Fig. 68. Ovotestis compact, darkly pigmented. Hermaphrodite duct short, nearly straight, with talon at short albumen gland. Spermoviduct slightly twisted, voluminous; prostatic gland ribbon-like, attached along axis of female oviducal tract. Free oviduct sinuous. Vagina absent. Reservoir of bursa copulatrix oval to globular, on duct arising from junction of penis and free oviduct. Atrium tubular. Euphallic individuals with phallus sinuous, elongate, its proximal apical part with several small papillae (phallus glands); stimulator in distal phallus small, hemispherical or obtusely conical. Vas deferens thin, long, opening into phallus laterally about 0.3 from apex.

Male copulatory organs often reduced, tending towards full aphally. Phallus often shorter, persisting as a broadening or swelling on atrium into which a shortened vas deferens opens; further reduction may lead to its complete

absence, the vas deferens becoming blind-ending, with no connection to atrium, or in the extreme with no free vas deferens. Female organs never reduced. Forms with reduced phallus somatically larger, with greater development of albumen gland and oviducal glands.

Phallus retractor muscle short, arising from diaphragm a little anterior to kidney, and inserted onto middle part of phallus.

Jaw (Fig. 109) of usual oxygnathous type, 1 mm in width.

Radular ribbon (Fig. M32–34) comprising about 80–110 rows of teeth, each varying in formula around 25+13+C+13+25. Central tooth with mesocone prominent, slender, flanked on either side by small, weak ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by a small endocone displaced towards mesocone tip and a small, pointed ectocone. Lateral teeth with mesocone progressively more slender, endocone becoming smaller and finally lost, and ectocone persisting until 11th to 18th tooth. Marginal teeth comprising only an elongate, slender mesocone, progressively smaller towards radular margin.

Digestive tract, Fig. 138. Buccal mass spheroidal. Oesophagus quickly expanding to large crop, which extends to about 0.6 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards a short distance to pass over anterior aorta, then producing a posterior loop nearly reaching body apex, before running forwards over stem of cephalic retractor to anus; rectum lacking a caecum.

Pallial complex (Fig. 165) located in posterior part of mantle. Kidney rounded to oval, its longer axis transverse relative to body axis, partially enclosing heart at its anterior margin; a lobe arising from ventral medial part and extending to right below rectum. Secondary ureter arising from right posterior aspect of kidney, describing an arc to right anterior quarter of pallial complex, where it terminates in a barrel-shaped bladder. Heart with ventricle axis slightly right-inclined. Aortic stem long, extending below kidney lobe and rectum to outside right pallial margin before dividing into anterior and posterior branches. Lung with vascular network poorly developed.

Free muscle system, Fig. 191. Cephalic retractor arising on body midline a little posterior to pallial complex, passing forwards as a long common stem; buccal retractors dividing off well anteriad from common stem, or occasionally from left tentacular branch.

Central nervous system (Fig. 219) with cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal than to cerebral ganglia. Visceral chain compact, with right pleural fused to right parietal ganglion; left parietal fused to visceral ganglion, which lies on median plane.

Type material. The whereabouts of the type material, from Frederiksdal, is unknown; it is presumed lost.

Distribution. *D. laeve* is a cosmopolitan terrestrial slug which has generally been assumed to be native to the Palearctic region. Chichester & Getz (1973) attribute the American distribution to natural spread in the Late Pleistocene or postglacial times. Van Regteren Altena (1966) and Barker & Pottinger (1983) considered the high mountains of Central America and the Andes of South America to be part of the natural range of *D. laeve*. This species has been introduced by man into most areas of the world.

Recommended common name. Marsh slug.

Material examined. New Zealand. AK. Henderson, 26 May 1987. Ellerslie, Sep 1980. Titirangi, Sep 1980 and 10 Oct 1993, associated with potted plants in nursery. **WO.** Gordonton, 11 Sep 1979 and 18 Aug 1992, associated with potted plants in nursery. Cambridge, Aug 1991, in greenhouse; Karapiro, Nov 1988, in cress beds on bank of stream. Ohaupo, 14 Jul 1983 and 17 Apr 1984, in greenhouse, associated with orchids.

Extralimital. Canada. Edmonton, Alberta, Jul 1986, in grass of *Salix* fen. **England.** Lashford Lane Fen Reserve, Oxfordshire, 22 Sep 1990, in swamp. **Fiji.** Nandarivatu, Viti Levu, Jan 1979, in vegetation on bank of forest stream. **Netherlands.** Haarlem, Oct 1990, in grasssland. Beekbergen, Oct 1990, in grass on canal bank. **Peru.** San Juan de Chuquibambilla, 3 Feb 1981, R.P. Pottinger, in pasture. Cusco, 12 Feb 1981, R.P. Pottinger, in pasture. **Poland.** Pin'czów, 13 Oct 1966, coll. & det. A. Wiktor. **Romania.** Balau, Oct 1967, coll. & det. D. Lupu. **U.S.A.** State College, Pennsylvania, May 1994, in pasture. **Vanuatu.** Aneityum, 1955, L.E. Cheesman (BMNH 1956.3.9.21-24).

History in New Zealand. In an earlier revision of introduced slugs Barker (1979) treated records of *D. laeve* in New Zealand by Musson (1891), Suter (1913), Thomson (1922), Whitten (1955), and Coleman (1970) as misidentifications of *D. panormitanum*. The current rather restricted distribution of *D. laeve* suggests that this species has only recently established in New Zealand and supports my earlier referral of records to *D. panormitanum*. However, Quick (1960) examined material of *D. laeve* from New Zealand, suggesting its presence here in the late 1950s.

Biology. *D. laeve* is remarkable for its unusually diverse habitats, spanning an enormous geographical and ecological range. It is known from sea level to over 3500 m altitude, and from Arctic tundra to mesic and tropical for-

ests and croplands. It is hygrophilic and, while occurring in other habitats, is most abundant in wetlands at the edge of streams, rivers, and lakes and in wet grasslands and forests. It is even partially amphibious (Pearl 1901, Chichester & Getz 1968, Wiktor 1983a, Rollo & Shibata 1991). In wetlands subject to periodic flooding *D. laeve* thrives while other species such as *D. reticulatum* are drowned (Rollo & Shibata 1991).

Another feature of *D. laeve* is its ability to survive freezing temperatures, and it is active over the range 0–30°C. This probably explains why its global range extends further northwards and southwards than that of *D. reticulatum*. Carrick (1942) and Karlin & Naegele (1960) claimed that immersion kills *Deroceras* eggs, but Rollo & Shibata (1991) found that *D. laeve* eggs develop normally and hatch underwater (see also Kosińska (1980) on *D. sturanyi*).

In New Zealand *D. laeve* is mostly restricted to the environs of nurseries, greenhouses, and gardens, but populations have been located in wet pastures and on stream banks in the Auckland and Waikato regions.

This species exhibits high plasticity in life history traits, with rapid growth and reproductive maturation within several months of hatching under favourable conditions, but with slow growth, delayed maturation, and extended lifespan under less favourable conditions. Mature slugs are thus always present to exploit unpredictable breeding opportunities in strongly seasonal, summer-dry climates, while in more equable situations breeding can be maintained throughout the year (Rollo & Shibata 1991). Little information is available on the life cycle in New Zealand, but dissection of material from several continuously wet stream bank habitats suggests that breeding occurs throughout the year.

Mating in *D. laeve* occurs under cover, such as beneath timber and stones. This species apparently does not engage in the courtship trail-following and circling seen in *D. reticulatum*. The copulatory position is maintained for up to 1 hour (Gerhardt 1939, and this study). The translucent grey eggs, with sparse calcareous crystals embedded in the coating, vary from 1.8x1.45 mm to 2.0x1.3 mm, and are deposited as early as 3 days after mating, on or in soil under logs, stones, and ground litter.

The male copulatory organs are frequently poorly developed (Baker 1930, Pilsbry 1948 (1939–48), Quick 1960, Wiktor 1973, Els 1978, Barker & Pottinger 1983). In euphallic individuals the phallus is a long tubular structure with internal stimulator and apical glandular papillae. With progression towards aphally the phallus may simply be shorter, or greatly reduced to a swelling on the atrium, and even completely absent, the blind end of the vas deferens having no connection with the atrium. In the extreme there is no free vas deferens. The female organs are never reduced. Forms with a reduced phallus are somatically larger, with the albumen gland and oviduct more strongly developed.

D. laeve has been reared in the laboratory uniparentally for many generations (e.g., Maury & Reygrobellet 1963). This, coupled with marked deficiencies of heterozygotes in natural populations, led Foltz *et al.* (1982b) and McCracken & Selander (1980) to suggest the occurrence of self-fertilisation. Nicklas & Hoffmann (1981) demonstrated parthenogenesis and outcrossing as facultative reproductive modes for this species. The low heterozygosity of uniparental laboratory and natural populations studied by Nicklas & Hoffmann (1981) has been attributed to automictic parthenogenesis by Hoffmann (1983). Further, the occurrence of populations of low genetic variability (as sampled by Foltz *et al.* 1982b, McCracken & Selander 1980), and others composed of single clones (Nicklas & Hoffmann 1981), led Hoffmann (1983) to suggest that there is geographic variation in the breeding system of the species, or that *D. laeve* consists of more than one cryptic species. Nicklas & Hoffmann (1981) were able to show that in their North American populations the variation in genital structure was affected by the temperature and photoperiod of the rearing environment.

Both euphallic and aphallic individuals are represented in New Zealand populations, with the latter strongly predominant.

D. laeve is omnivorous, with a proclivity for supplementing its diet of living plants and litter with faeces, carrion, and even living animals. It is opportunistically predaceous on slow-moving animals such as earthworms, aphids, mealybugs, and insects caught in spider webs (Karlin & Naegele 1960, Quick 1960, Fox & Landis 1973, Rollo *in* Rollo & Shibata 1991), is highly aggressive towards other molluscs, and is cannibalistic (Karlin & Naegele 1960, Rollo & Wellington 1979). Reports on *D. laeve* as a pest of cultivated plants have been largely confined to floriculture (e.g., Alicata 1950).

Remarks. As a consequence of the great geographical range of this slug, numerous specific names have been erected. Little has changed since Baker (1930, pp. 41–42) remarked "... none of the describers or revisers of the names included in the foregoing synonymy [of *D. laeve*] has ever contributed satisfactory proof towards the separation of any of them from *D. laeve* of Europe"; or Meeuse & Hubert (1949, p. 25): "The relationship of the various forms which are usually included in *D. laeve*, but which have so far not been conclusively proved to belong to one and the same species, is far from clear." In Europe at least, until recently *D. laeve* has been confused with *D.*

sturanyi (Simroth 1894) (Wiktor 1973, 1983b).

Several variety names are to be found in the literature (e.g., Quick 1960), relating to variations in body coloration.

Important references to *D. laeve* are Germain (1930), Pilsbry (1948 (1939–48)), van Regteren Altena (1950), Likharev & Rammel'meier (1952), Quick (1960), Ellis (1967), Bequaert & Miller (1973), Wiktor (1973, 1983a, 1989), Backhuys (1975), Likharev & Wiktor (1980), and Barker & Pottinger (1983).

Deroceras (Deroceras) panormitanum (Lessona & Pollonera)

Figures 26, 29, 69, 110,139, 166, 192a, b, 220a, b, 245, C2, M35–37; Map 2

agrestis of authors (not of Linnaeus, 1758).
laeve of authors (not of Müller, 1774).
panormitanum Lessona & Pollonera, 1882: 52 (*Limax*, sect. *Agriolimax*).
queenslandicus Hedley, 1888: 150 (*Limax*).
pollonerae Simroth, 1889a: 179 (*Agriolimax*).
caruanae Pollonera, 1891: 3 (*Agriolimax*).
cecconii Pollonera, 1896: 6 (*Agriolimax*).
agrestis var. *nigra* of authors (not of Morelet, 1845).
agrestis var. *violacea* of authors (not of Gassies, 1849).
cecconii var. *ilvatica* Pollonera, 1905: 3 (*Agriolimax*).
dubius Hoffmann, 1941: 254 (*Agriolimax*).
meridionalc Reygrobellet, 1963: 399 (*Deroceras*).

Slugs (Fig. 26) up to 30 mm in length, slim, posteriorly obtusely narrowing, with keel short and ill defined. Mantle shield about 0.4 of body length. Body wall thin and transparent, chocolate brown, grey, or black, unicoloured in appearance but under magnification seen to be speckled or flecked. Border of pneumostome pale. Sole pale grey. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 29) thin, white, oblong-oval to ovoid but with right margin commonly concave, up to 4.6 × 2.8 mm in size. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, non-protruding, situated asymmetrically at left side or less frequently on midline. An organic sheet surrounds the shell.

Reproductive system, Fig. 69. Ovotestis rather large and darkly pigmented, partly exposed in viscera on the left, somewhat forward of hind body apex. Hermaphrodite duct short, nearly straight, with talon partially embedded in short albumen gland. Spermoviduct slightly twisted, voluminous. Prostatic gland ribbon-like, attached along axis

of female oviducal tract. Free oviduct sinuous. Vagina absent. Bursa copulatrix reservoir oval, on a duct arising from junction of phallus and free oviduct. Atrium tubular, short. Phallus large, distorting anterior body wall of mature animals, distinctly divided by a medial narrowing into 2 parts: proximal part with a phallus gland of 4–6 slender, smooth or crenulate flagella located in a shallow recess between phallus lobe and digitiform phallus caecum; anterior part with a strong bulbous, glandular lateral outgrowth, narrowing to atrium, and internally with a conical sarcobelum. Vas deferens thin, opening into phallus at base of caecum adjacent to phallus gland flagella.

Phallus retractor muscle short, arising from diaphragm at anterior margin of kidney or a little forward, inserted onto proximal part of phallus at base of caecum adjacent to entry of vas deferens.

Jaw (Fig. 110) of usual oxygnathous type, 1.3 mm wide.

Radular ribbon (Fig. M35–37) comprising about 90–110 rows of teeth, each varying in formula around 34–55+14–18+C+14–18+34–55. Central tooth with mesocone prominent, slender, flanked on either side by short, prominent ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by a small, weak endocone displaced towards mesocone tip and a prominent ectocone. Lateral teeth with mesocone progressively more slender, endocone becoming smaller and finally lost, and an ectocone often persisting in first few marginal teeth. Marginal teeth mostly comprising only an elongate, slender mesocone, progressively smaller towards radular margin.

Digestive tract, Fig. 139. Buccal mass spheroidal. Oesophagus quickly forming a large crop, which extends to about 0.6 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards a short distance to pass over anterior aorta, then producing a posterior loop nearly reaching hind apex of body, before running forwards over stem of cephalic retractor to anus. Rectum with a small caecum.

Pallial complex (Fig. 166) located in posterior part of mantle. Kidney rounded to oval, its longer axis transverse relative to body axis, almost entirely enclosing heart at its anterior margin; a lobe arising from ventral medial part and extending to the right below rectum. Secondary ureter arising from right posterior aspect of kidney, describing an arc to right anterior quarter of pallial complex, where it terminates in an oval bladder. Heart with ventricle axis slightly right-inclined. Aortic stem long, extending below kidney lobe and rectum to outside right pallial margin before dividing into anterior and posterior branches. Lung with vascular network poorly developed.

Free muscle system, Fig. 192a, b. Cephalic retractor arising on body midline a little posterior to pallial complex, passing forwards as a long common stem; buccal retractors anteriorly dividing off from left tentacular branch.

Central nervous system, Fig. 220a, b. Cerebral ganglia united by a commissure in length about equal to cerebral ganglion width. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact, with right pleural ganglion fused to right parietal; left parietal fused to visceral ganglion, which lies on median plane.

Type material. The whereabouts of the type material, from Palermo, Sicily, is not known.

Distribution. Originating in SW Europe, *D. panormitanum* has been spread to many parts of Europe, the Canary Islands, southern Africa, North and South America, Australia, and New Zealand.

Recommended common name. Brown field slug.

Material examined. New Zealand. Kermadec Is. Raoul I., Denham Bay, Feb 1973, J. Ireland, in forest litter (MONZ M137923). Raoul I., Beacon Flat, 9–22 Sep 1973, J. Ireland, in forest litter (MONZ M137913, -914, -925). Mt Moumoukai, 1 Dec 1972, J. Ireland, in forest litter (MONZ M137902). **ND**. Rangi Point, Jan 1991. Kohukohu, Jan 1991, in grass at forest edge. Horeke, Jan 1991. Kerikeri, 14 Jul 1977, B.J. Greaney. Paihia, 11 Aug 1974, M.A. Cumber. Maunganui Bluff, Jan 1991, in gardens and grassy area of coastal cliffs. Apotu, 1 Nov 1978. **AK**. Te Hana, 23 Feb 1994, in pasture. Leigh, Goat I. Bay, 5 Dec 1979, B.F. Hazelwood, under *Phormium* on coastal bank. Otakairangi, 21 Oct 1978, in pasture. Glen Eden, 29 Oct 1977, M. Lessiter, associated with potted plants in nursery. Titirangi, 29 Oct 1977, G.W. Ramsay. Ellerslie, 18 Oct 1977, J.C. Curd & R.M. Edwards. Mt Wellington, 15 Aug 1977, R.M. Edwards. **CL**. Whangamata, 25 Nov 1977, C.A. Scott. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. **WO**. Tahuna, 25 May 1976 and 26 May 1977, in maize stubble. Ohinewai, 18 Jul 1977, in pasture. Taupiri, 18 Jul 1977, in weedy roadside parking area. Glen Massey, 20 Apr 1977, in pasture. Whatawhata, 21 Dec 1993 and 3 Jan 1994, in pasture. Komakorau, 18 Jul 1977, in grassy area at roadside. Tauwhare, 24 Feb 1995, in pasture. Matangi, 18 Jul 1980, R.N. Watson, in commercial asparagus stand. Hamilton, 7 Mar 1976, 10 Sep 1976, 7 Jan 1977, 28 Apr 1977, 6 Jun 1977, 24 Oct 1977, 5 Jan 1978, 29 Jun 1978 and 21 Sep 1978, in gardens and pasture. Te Kowhai, 19 Sep 1978, in pasture. Rukuhia, 24 May 1976 and 8 Jan 1977, in pasture. Te Uku, 16 Jul 1977, in pasture and adjacent forest margin. Raglan, 22 Jan 1977 and 16 Jul 1977, in swampy area of rear dunes. Ruapuke, 27 Jan 1996, in coastal broadleaf forest. Horo Horo, 2 Jul 1977, in grassy area at lake edge. Hinuera, Dec 1992, in grassy area at margin of *Dacrycarpus dacrydioides* forest remnant. Ohaupo, 8 Nov 1992, 15 Mar 1993 and 8 Mar 1994, in pasture and garden. Ngaroto, 7 Nov 1992, in pasture and grassy area at margin of *Dacrycarpus dacrydioides* forest remnant. Pirongia, 19 Sep 1978. Tokoroa, 8 Jan 1979, U.J. Crocker. Rangitoto, 28 Mar 1977 and 8 Jun 1977, in pasture. Waitomo, 19 Sep 1978, under limestone rocks in pasture. Oparure, 19 Dec 1977 and 21 Sep 1978, under limestone rocks in pasture. Mairoa, 8 Jun 1977 and 6 Aug 1977, in pasture. Piopio, 28 May 1977, in pasture. **BP**. Mt Maunganui, 12 Sep 1986, in garden. Lower Kaimai, 25 Jun 1977 and 27 Dec 1977, in pasture and garden. Matata, 12 Sep 1986, in swampy area at rear of dunes. Opotiki, 13 Sep 1986, in gardens. Whangaparaoa, 14 Sep 1992, in dunes, associated with *Carex* and *Cyperus*. Raukokore, 15 Sep 1992. Potaka, 16 Sep 1992. Hicks Bay, 18 Nov 1977 and 20 Sep 1992, in disturbed, open areas of *Beilschmiedia tawaroa-Vitex lucens* coastal forest. Tarawera, Dec 1988, in gardens. Rotoma, 29 May 1977, in grassy area at forest margin. Manawahe, 26 Mar 1977, in garden. Mamaku, 25 Jan 1996, in broadleaf scrub. **TO**. Arohena, Waipapa Scenic Reserve, 25 Jan 1996, in *Leptospermum* scrub. Reporoa, 4 Mar 1994, in pasture. Aratiatia, 25 Jan 1996, in broadleaf scrub. **GB**. Te Araroa, 21 Sep 1992, under drift logs on gravel dune. Waioroho, 17 Sep 1992, in pasture and opens areas in *Dacrycarpus dacrydioides* forest. Rangiata, 20 Sep 1992, in litter of disturbed *Dysoxylum spectabile-Vitex lucens-Beilschmiedia tawaroa* forest. East Cape, 20 Sep 1992, under fallen *Rhopalostylus sapida* fronds in disturbed coastal *Vitex lucens-Beilschmiedia-Dysoxylum spectabile* forest. Whangara Valley, 16 Nov 1977, in pasture. Gisborne, 3 Nov 1978, N. Harding. **TK**. Te Wera State Forest, 15 Feb 1978, M. Stoodley. Normanby, 13 Dec 1977, W.J. Pengelly, in pasture. Hawera, 1 Dec 1977 and 15 Dec 1977, W.J. Pengelly, in pasture. Otangi, 13 Jul 1988, I. Townsend. Waihi Beach, 23 Apr 1978. **HB**. Hastings, 7 Jan 1978 and 19 Jan 1978, T.H. Davies. **WI**. Bulls, May 1977, W. Stiefel, in pasture. Palmerston North, 15 Jan 1978, M.A. Stoodley. **WN**. Levin, Jun 1977, J.W. Dobson. Upper Hutt, 15 May 1991, in disturbed *Beilschmiedia tawa* forest. Wellington, 29 Aug 1978, M. Peters. **WA**. Masterton, 27 May 1977, G. Crouchley, in pasture. Blairlogie, 27 May 1977, G. Crouchley, in pasture. **NN**. Mapua, 3 Jan 1978, J. Marris. **BR**. Totara Flat, Apr 1977, J.D. Morton, in pasture. **KA**. Lyndon, Dec 1979, P.C. Mayhill. **MC**. Christchurch, 18 Oct 1977, J.C. Curd. Christchurch, 8 Jan 1978, K. Marcussen. Christchurch, 21 Sep 1991, L. Ford. Ashburton, 10 Dec 1976 and 4 Apr 1977, J. Wood, in pasture. **WD**. Kokatahi, Apr 1977, J.D. Morton, in pasture. **SC**. Seadown, Feb 1977, C.M. McLeod. Kerrytown, Feb 1977, C.M. McLeod, in pasture. Washdyke, 8 Feb 1977, C.M. McLeod, in pasture. Claremont, Feb 1977, C.M. McLeod, in pasture. Timaru, 8 Feb 1977, C.M. McLeod, in pasture. **DN**. Portobello, 16 Feb 1994, in grassy area at harbour edge. Mosgiel, Sep 1982, T.G. Watson, in pasture. Mosgiel, 15 Feb 1994, in pasture. **Chatham Is**. Waitangi, 29 Sep 1976, in pasture. Pitt I., 1 Oct 1976, in pasture.

Extralimital. Australia. Sydney, New South Wales, Oct 1993, in gardens. **Brazil**. Porto Alegre, Rio Grande do Sul, 20 Aug 1991, in park. Parque do Caracol, Canela, Rio Grande do Sul, 21 Aug 1991. **Ireland**. Killarney, Kerry, 24 Aug 1990. **Scotland**. Auchincruive, Dumfries & Galloway, 12 Sep 1990, in gardens. **South Africa**. Stellenbosch, Cape Province, 1978, W.F. Sirgel.

History in New Zealand. *D. panormitanum* was first recognised in the New Zealand fauna by Barker (1979). It had long been established here (see also Barker 1992), but was apparently misidentified as *D. laeve* by Musson (1891), Longstaff (1912), Suter (1913), Thomson (1922), Whitten (1955), and Coleman (1970).

Biology. *D. panormitanum* is a slug of moist habitats, found in gardens, parks, and pastures, on arable land, stream banks, and roadsides, and in greatly disturbed areas of native forest.

Breeding apparently occurs throughout the year provided that moist conditions prevail. Mating has been described by Gerhardt (1939), Quick (1960), and Webb (1961b, 1965), and mating behaviour observed in New Zealand (Fig. 245) is in agreement with these accounts.

Courtship begins with a clockwise circling movement of two animals. As this circling continues, the sarcobela are protruded and the animals engage in biting each other's tail end. In some matings, intermittent slow circling occurs between periods of static tail-wagging and biting. After some 20–30 minutes the slugs come to rest alongside each other head-to-tail, with the body more or less curved, and the stimulators held rigidly turgid. In many instances, slugs at this stage of mating keep the head and tail uplifted and lunge laterally with the head to bite the other's flank and tail. The recipient of the bites often responds with violent side-to-side lashing of its tail, impacting against the anterior body of the aggressor. The strong arching and biting thrusts of the head result in the rigid stimulator-tip brushing swiftly along the flank of the other slug. As noted by Webb (1961b), in this movement the stimulator seems more frequently to contact the mate than the biting mouthparts. In the final phase of this precopulatory behaviour the stimulators become somewhat shortened. The slugs then reciprocally crawl forwards along the right side of the other until the atria but not the stimulators become contiguous. As soon as this body position is reached, the proximal lobe of the phallus is rapidly everted and entwined with the corresponding part from the other slug.

A period of 10–15 minutes of relative inactivity follows, broken by the sudden eversion and entwistment of the semen-bearing medial lobe of the phalluses. These medial lobes then begin to shrink, accompanied by rapid eversion of the phallus flagella, which when fully everted extend radially out like the fingers of a hand. The sex organs then soon become completely separated, and the phalluses continue to shrink and introvert. The animals separate, but complete introversion of the phallus structures to the precopulatory position, particularly that of the sarcobela, is not attained for some 30 minutes or more.

Webb (1961b, 1965) dissected animals shortly after mating and found that the semen received occupies the medial part of the phallus near the bursa copulatrix duct insertion. Semen was noted to have been almost entirely transferred into the bursa copulatrix system in an animal examined 8 minutes after copulation.

Gregg (1944) reported fertile eggs from unmated slugs of this species, and is supported by Quick (1960), who noted that individuals isolated from birth occasionally laid a few viable eggs.

The eggs vary from spherical, approx. 1.5 mm in diameter, to oval 1.75x1.4 mm, and are translucent grey with little or no calcareous crystal content.

As noted by Quick (1960), *D. panormitanum* is an active, rather fast-moving slug. It displays an irritable and pugnacious behavioural trend, frequently biting and tail lashing at its neighbours.

D. panormitanum feeds on a variety of living and decaying plant material and is often important as a pest in pastures, nurseries, greenhouses, gardens and commercial crops such as asparagus and lettuce. It has strong cannibalistic tendencies, even when food is plentiful. Conspecifics weakened by molluscicide poisoning have been noted to be particularly favoured victims of such cannibalism.

Remarks. The taxonomic status of *D. panormitanum* has long been disputed. After critical examination of the orginal descriptions, type specimens, and fresh material from various European localities, Giusti (1973, 1976, 1986) has placed *D. pollonerae* (Simroth, 1889) and *D. caruanae* (Pollonera, 1891) as junior synonyms. On the morphology of body, radula, and phallus complex these three nominal taxa cannot be clearly distinguished one from another. There has been much specific radiation of *Deroceras* in Europe, and Giusti (1986) has stressed that his proposed synonymy does not necessarily involve all populations.

Important references to *D. panormitanum* are Pilsbry (1948 (1939–48)), van Regteren Altena (1950, 1966), Quick (1960), Ellis (1967), Giusti (1973, 1976, 1986), van Goethem (1974), Backhuys (1975), Likharev & Wiktor (1980), Wiktor (1983a), van Goethem & de Wilde (1985), Alonso *et al.* (1986), Cesari (1988), Giusti & Manganelli (1990a), and Wiktor *et al.* (1994).

Subgenus *Agriolimax* Mörch

Agriolimax Mörch, 1865: 378, type species *Limax agrestis* Linnaeus, 1758, designated by Malm (1868).
Chorolimax Westerlund, 1894 (1892–94): 163, type species *Limax agrestis* Linnaeus, 1758, by original designation.

Diagnosis. Body stout. Mantle 0.3 of body length in extended slugs, the posterior edge not attaining half of body length. Skin thick, not transparent. Phallus short, spherical or with a fissure in middle; proximal end with a gland in the form of a single or branched appendix, but other accessory structures absent; distal part with a conical sarcobelum, narrowed apically, less frequently flattened laterally. Rectal caecum usually several times longer than wide, exceptionally in the form of a shallow pocket.

Deroceras (Agriolimax) reticulatum (Müller)

Figures 27, 30, 70, 111, 140, 167, 193, 221, 246, C3, M38–40; Map 3

agrestis of authors (not of Linnaeus, 1758 as restricted by Luther, 1915).
laeve of authors (not of Müller, 1774).
reticulatum Müller, 1774: 10 (*Limax*).
canariensis d'Orbigny, 1839 (1836–42): 47 (*Limax*).
tunicata Gould, 1841: 3 (*Limax*).
niger Morelet, 1845: 34 (as var. of *agrestis* Linnaeus) (*Limax*).
violacea Gassies, 1849: 64 (*Limax*).
minutus de Kaleniczenko, 1851: 224 (*Krynickillus*).
molestus Hutton, 1879: 331 (*Limax*).
niciensis Nevill, 1880: 103 (*Krynickillus*).
? *simrothi* Cockerell, 1893: 176 (*Agriolimax*).
pallidus of authors (not of von Schrank, 1848).
altenai Lupu, 1976: 10 (*Deroceras*).

Slugs (Fig. 27a–e) of extended length up to 50 mm, stout, posteriorly obliquely truncated, with a short, ill defined keel. Mantle shield about 0.3 of body length. Body wall thick, usually cream or pale brown, with blackish or brown spots distributed mainly in the skin grooves. Mantle similarly cream or pale brown, flecked or spotted black or brown. Pigmentation varying within populations from wholly dark to pale specimens. Border of pneumostome pale. Sole usually creamy, but brown in intensely coloured specimens. Mucus clear in undisturbed animals, but milky on irritation. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 30) thin, white, oblong-oval to ovoid but with right margin commonly convex, up to 5.5x3.8 mm in size. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, non-protruding, situated asymmetrically at left side. An organic sheet surrounds the shell.

Reproductive system, Fig. 70. Ovotestis elongate, lying at or near apex of body cavity, partially exposed dorsally in viscera. Hermaphrodite duct short, with talon at its termination in linguiform albumen gland. Spermoviduct somewhat folded, broadest at proximal part; female part terminating in a straight or weakly contorted free oviduct; prostatic gland as a ribbon along entire glandular oviducal tract, giving rise to short vas deferens. Phallus rather large, with thick walls and a fissure in middle; phallus gland on proximal part a single, slightly flattened flagellum or consisting of several flagella branching from a very short stem; flagella always covered with nodulose glandular papillae. Vas deferens opening through phallus wall adjacent to body wall, a little below phallus gland. Bursa copulatrix reservoir oval to globular, opening into distal phallus via a short duct.

Phallus retractor muscle short, arising from diaphragm a little anterior of kidney, inserted onto medial region of phallus.

Jaw (Fig. 111) oxygnathous, 1.4 mm wide.

Radular ribbon (Fig. M38–40) with 80–125 transverse rows of teeth, each with the formula varying around 21–32+16–22+C+16–22+21–32. Central tooth with mesocone elongate, slender, flanked by shorter but prominent ectocones. Lateral teeth with mesocone more robust but equally long, a small endocone displaced towards tip of mesocone, and a small but prominently pointed ectocone, progressively more elongate and grading into sword-like marginal teeth. Marginal teeth progessively smaller towards radular margin, with endocone sometimes persisting in first few teeth, and ectocone frequently persisting as a minute cusp in teeth at radular margin.

Digestive tract, Fig. 140. Buccal mass spheroidal. Oesophagus quickly expanding to large crop, which extends about 0.6 length of body cavity. Stomach a simple curvature, with 2 ducts to the digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards a short distance to pass over anterior aorta, then producing a posterior loop extending below stomach to nearly reach the body apex, and finally running forwards over stem of cephalic retractor to anus. Rectal caecum well developed, several times longer than wide, lying dorsally over viscera.

Pallial complex (Fig. 167) located in posterior part of mantle. Kidney rounded to oval, its longer axis transverse relative to body axis, partially enclosing heart at its anterior margin; a lobe arising from ventral medial part and extending to the right below rectum. Secondary ureter arising from right posterior aspect of kidney, describing an arc to right anterior quarter of pallial complex, where it

terminates in a barrel-shaped bladder. Heart with ventricle axis slightly right-inclined. Aortic stem long, extending below kidney lobe and rectum to outside right pallial margin before dividing into anterior and posterior branches. Lung with vascular network poorly developed.

Free muscle system, Fig. 193a–c. Cephalic retractor arising on body midline a little posterior to pallial complex, commonly dividing from its root to form right ocular retractor and a common stem for left ocular and buccal retractors. Variants occur with stem united before branching anteriad to right and left ocular retractors, and with buccal retractor arising near origin or at fork of ocular retractors.

Central nervous system, Fig. 221a, b. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal ganglion fused with right pleural; left parietal fused with visceral ganglion, which lies to left of median plane.

Type material. Described from material from Frideriksdal near Copenhagen, Denmark. The holotype probably no longer exists. Topotypic specimens are described and illustrated by van Regteren Altena (1969).

Distribution. This European slug has been widely dispersed through the activities of man, and its natural range is not known. Occurring partly as a native and partly as a synanthrope, *D. reticulatum* is the most common slug in the whole of northern and central Europe. It is less common in southern Europe, where it is replaced by other species (Wiktor 1983a). Introduced and established widely, including North and South America, South Africa, islands of the Atlantic and Indian oceans, Australia, and New Zealand.

Recommended common name. Grey field slug.

Material examined. New Zealand. ND. Stephenson I., June 1992, R. Parrish. Kerikeri, 14 Dec 1977, B.J. Greaney. Paihia, 11 Aug 1974, M.A. Cumber. Rangi Point, Jan 1991. Maunganui Bluff, Jan 1991, in gardens. Apotu, 1 Nov 1978. Otakairangi, 1 Nov 1978 and 27 Jul 1993, R. Parrish. Matarau, 1 Nov 1978, in pasture. Whangarei, 5 Aug 1977, C.A. Sanders. Whangarei, 1 Nov 1978, in park. Parua, 2 Nov 1978. **AK.** Te Hana, 23 Feb 1994, in pasture. Otakinini, 20 Oct 1978, in pasture. Glen Eden, 19 Oct 1977, M. Lessiter. Titirangi, 27 Oct 1977, G.W. Ramsay. Ellerslie, 18 Oct 1977, J.C. Curd & R.M. Edwards. Mt Wellington, 15 Aug 1977, R.M. Edwards. Pukekohe, Jul 1974, N.A. Martin. **CL.** Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. **WO.** Tahuna, 25 May 1976 and 26 May 1977, in maize stubble and in pasture. Ohinewai, 18

Jul 1977, in pasture. Taupiri, 18 Jul 1977, in pasture. Tauwhare, 15 Dec 1994, in pasture. Te Miro, 19 Apr 1977, in grassy area at forest margin. Glen Massey, 20 Apr 1977, in pasture. Te Poi, 2 Jul 1977, in grassy area at roadside. Whatawhata, 21 Dec 1993 and 3 Jan 1994, in pasture. Matangi, 18 Jul 1980, R.N. Watson, in commercial asparagus stand. Hamilton, 7 Mar 1976, 24 May 1976, 7 Jan 1977, 28 Apr 1977, 21 Aug 1977, 24 Oct 1977, 12 Nov 1977, 29 Jun 1978 and 20 Sep 1978, in pasture and gardens. Rukuhia, 15 May 1977 and 20 Jul 1978, in pasture. Karapiro, Mar 1992, in pasture. Hinuera, Dec 1992, in pasture. Te Kowhai, 19 Sep 1978, in pasture. Moanatuatua, 9 Oct 1977, in pasture. Ohaupo, 8 Nov 1992, 15 Mar 1993 and 8 Mar 1994, in pasture and gardens. Te Uku, 16 Jul 1977, in pasture. Raglan, 16 Jul 1977, in gardens. Ruapuke, 27 Jan 1996, in coastal broadleaf forest and pasture. Karamu, 27 Jan 1996, in broadleaf scrub and pasture. Te Mata, Bridal Veil Falls Scenic Reserve, 27 Jan 1996, in broadleaf scrub. Ngaroto, 7 Nov 1992, in pasture. Waikeria, 11 Jan 1977, in pasture. Pirongia, 22 Mar 1977 and 19 Sep 1978, in pasture. Tokoroa, Jul 1977 and 8 Jan 1979, V.J. Crocker. Waitomo, 11 Sep 1976, 10 Jan 1977 and 19 Sep 1978, in pasture. Rangitoto, 8 Jun 1976 and 14 Apr 1977, in pasture. Oparure, 19 Dec 1977, in pasture. Mairoa, 8 Jun 1976, in pasture. Piopio, 28 May 1976, in pasture. **BP.** Lower Kaimai, 25 Jun 1977 and 9 Sep 1978, in pasture and garden. Tauranga, 5 Dec 1977, R.J. Bell. Te Puke, 6 Jul 1989, C. Marshall, in pasture. Opotiki, 12 Sep 1986, in gardens. Whangaparaoa, 14 Sep 1992, G.M. Barker & P.C. Mayhill, in exotic grasses of dunes. Raukokore, 15 Sep 1992, in disturbed coastal *Beilschmiedia tawaroa-Vitex lucens* forest. Potaka, 16 Sep 1992. Hicks Bay, 20 Sep 1992, in pasture. Mamaku, 25 Jan 1996, in broadleaf scrub and grassy roadside. Tarawera, 6 Dec 1988, in gardens. Rotoma, 29 May 1977, in grassy area at forest margin. Manawahe, 22 Nov 1976, in pasture. Otara, 31 Jul 1974, in pasture. **GB.** Waioroho, 17 Sep 1992, in pasture. Te Araroa, 21 Sep 1992, in grassy areas of gravel dunes. Whangara Valley, 16 Nov 1977, in pasture. **TO.** Waiotapu, 25 Jan 1996, in grassy forest firebreak. Reporoa, 4 Mar 1994, in pasture. Aratiatia, 25 Jan 1996, in broadleaf scrub. Taupo, 3 Jun 1976, in pasture. **TK.** Te Wera State Forest, 15 Feb 1978, M. Stoodley. Normanby, 13 Dec 1977, W.J. Pengelly, in pasture. Hawera, 1 Dec 1977 and 15 Dec 1977, W.J. Pengelly, in pasture. Ohangai, 13 Jul 1988, I. Townsend, in greenhouses and adjacent pasture. **HB.** Napier, 1 Nov 1978, R.F. Lowe. Hastings, 7 Jan 1978, T.H. Davies. **WI.** Bulls, May 1977, W. Stiefel, in pasture. Whangaehu Valley, Mar 1977, G. Crouchley, in pasture. Blairlogie, 27 May 1977, G. Crouchley, in pasture. **WN.** Levin, Jun 1977, J.W. Dobson. Upper Hutt, 15 May 1991, in park. **NN.** Nelson, 12 Sep 1977, G.B. Radford. Mapua, 24 Apr 1978, J. McPherson. Aniseed Valley, 18 Jul 1978, C.C. Meikle. Westport, Apr 1977, J.D. Morton, in pasture. **BR.** Ahaura, Apr 1977, J.D. Morton, in pasture. Mawheraiti, Apr 1977, J.D. Morton, in pasture. Kokiri, Apr 1977, J.D. Morton, in pasture. **KA.** Lyndon, Dec 1991, in pasture. **MC.** Craigie Burn, 3 Apr 1978, D.W. Burton. Christchurch, 18 Oct 1977, J.C. Curd. Christchurch, 6 Dec 1977, L.S. Hanser. Christchurch, May 1988. Halswell, Nov 1976, R. Blank. Ashburton, Jan 1977, 4 Apr 1977 and 10 Dec 1977, J. Wood. **WD.** Otira, May 1990, H. White. **SC.** Levels, 3 Feb 1977, C.M. McLeod, in pasture. Timaru, 4 Mar 1977, C.M. McLeod, in pasture. Kerrytown, Mar 1977, C.M. McLeod, in

pasture. Claremont, Feb 1977, C.M. McLeod, in pasture. Mt Dasher, Dec 1962, P.M. Johns. **DN**. Palmerston, 19 Dec 1977, S.M.J. Stockdill, in pasture. Dunedin, Dec 1977, H. McAllan. Flagstaff, 16 Feb 1994, in grassy area in *Pinus* plantation. Portobello, 16 Feb 1994, in grassy area at harbour edge. Mosgiel, Sep 1982, T.G. Watson, in pasture. Mosgiel, 15 Feb 1994, in pasture. **CO**. Millers Flat, Aug 1977, B.I.P. Barratt, in oversown tussock grassland. Rocklands, Sep 1982, B.I.P. Barratt & G.M. Barker, in oversown tussock grassland. **SI**. Halfmoon Bay, Jan 1979, P.C. Mayhill. **Chatham Is**. Waitangi, 27 Sep 1976, in pasture. Pitt I., 30 Sep 1976, in pasture. **Auckland Is**. Port Ross, 8 Nov 1954, E.S. Gourlay, on *Dracophyllum longifolium* (BMNH). **Campbell I.** 26 May 1942, J.H. Sorensen (AMNZ).

Extralimital. Australia. Ballarat, Victoria, Sep 1988, in pasture. Melbourne, Victoria, Oct 1993, in market garden. Scottsdale, Tasmania, Oct 1993, in pasture. **England**. Bucks Horn Oak, Farnham, Hampshire, 18 Nov 1990, in oak woodland. Maidenhead Thicket, Berkshire, 28 Apr 1990, in grassland. **Ireland**. Killarney, Kerry, 24 Aug 1990. **Netherlands**. Amsterdam, Oct 1990, in grass on canal bank. **Peru**. Cusco, 12 Feb 1981, R.P. Pottinger, in pasture. **Poland**. Dolina Lomniczki, Karkonosze Mtns, 28 Oct 1963, coll. & det. A. Wiktor. **Romania**. Tareau-Nearut, 29 Oct 1959, coll. & det. D. Lupu. **Scotland**. Auchincruide, Dumfries & Galloway, 22 Sep 1990, in grass at roadside. **South Africa**. Stellenbosch, Cape Province, 1978, coll. & det. W.F. Sirgel. **Spain**. Muros, Galicia, Apr 1989, in grassland. Ponferrada, Galicia, Apr 1989, in pasture. **U.S.A**. Newcastle, Pennsylvania, May 1994, in pasture. **Wales**. Merthyr Tydfil, Mid Glamorgan, 29 May 1990, open woodland.

History in New Zealand. *D. agreste* has repeatedly been said to occur in New Zealand (e.g., Hutton 1881, 1882b, 1883, Musson 1891, Suter 1891, 1913, Hedley & Suter 1893, Taylor 1902–07 (1902–21), Whitten 1957), but was not found among the large amount of material examined in the course of this or an earlier revision (Barker 1979) of the introduced slugs. It appears that the earlier records of *D. agrestis* were misidentifications of *D. reticulatum*, or simply that the authors of the time did not recognise *D. reticulatum* as a valid species name. Taylor (1902–07 (1902–21)), for example, recorded from New Zealand *violacea* Gassies, 1849, *niger* Morelet, 1845, and *pallida* Schrank, 1848 as varieties of *D. agreste*. Quick (1960) considered *violacea* and *niger* (as *nigra*) to be varieties of *D. reticulatum*, while Hesse (1926) and Wiktor (1983a) considered *pallida* a variety of *D. agreste* s.s. The situation is further complicated by the fact that *D. agreste* in the sense of Taylor (1902–07 (1902–21)) is now recognised as comprising *D. agreste*, *D. reticulatum*, and *D. panormitanum*.

As *D. panormitanum* has long been established in New Zealand, it is probable that the darkly pigmented varieties *niger* and *violacea* recorded from this country by Taylor refer, at least in part, to this species. However, Taylor considered *Agriolimax panormitanum* Lessona & Pollo-

nera, 1882 to be a junior synonym of *Limax agrestis* var. *niger* Morelet, 1845. Whitten (1957) recognised that his earlier (Whitten 1955) records of *D. agreste* (as *Agriolimax*) in New Zealand were referable to *D. reticulatum*.

Limax molestus Hutton, 1879, described from New Zealand material, was previously referred to *D. reticulatum*, since Hutton's brief description is most consistent with Müller's species (Barker 1979); the holotype of *L. molestus* has not been examined. Hutton himself (1881, 1883) reduced *L. molestus* to synonymy with *D. agreste* (= *D. reticulatum* (Müller, 1774)) (not of Linnaeus 1758), and this was followed by Suter (1913). By contrast, Grimpe & Hoffmann (1925) listed *L. molestus* as a synonym of *D. laeve* (Müller, 1774).

Quick (1960) examined material of this species from New Zealand.

Biology. *D. reticulatum* shows wide ecological tolerance, but always living in open or poorly wooded habitats and never in closed forests. It occurs most frequently and abundantly in ruderal environments, refuse heaps, gardens and parks, ditches and roadsides, arable fields, and grazed pastures.

Because of its utility as a laboratory animal and its frequent pest status in cultivated crops there is an extensive literature on *D. reticulatum*. For an introduction to its biology and behavioural ecology in Europe and North America the reader is referred to Carrick (1938, 1942), Getz (1959), Arias & Crowell (1963), Newell (1966), Dmitrieva (1969), Hunter (1968, 1978), Runham & Laryea (1968), Crawford-Sidebotham (1972), and South (1965, 1982, 1989a, b).

D. reticulatum is the most widely distributed and generally the most abundant slug in modified habitats in New Zealand, occurring throughout the North and South islands and on Stewart, Chatham, Auckland, and Campbell islands. In outdoor gardens and nurseries, arable crops, and pasture it is often of pest status. In recognition of this pest status in agriculture (Barker 1989), the population biology (Barker 1991a) and damage potential (Charlton 1978a, b, Ferguson & Barratt 1983, Barker 1990, 1991b, Barker et al. 1990, Barker & Addison 1992) of this species have been extensively studied in pasture situations. Information on its biology and the losses inflicted on other agricultural crops is incomplete, but is available for asparagus (Watson 1980, Watson & Townsend 1981) and no-tillage cereals (Barker et al. 1984, Hughes & Gaynor 1984). While its reproductive phenology can vary according to the microenvironmental conditions of a particular habitat, *D. reticulatum* is generally most reproductively active and in greatest abundance in autumn and, more especially, spring.

D. reticulatum is a heterozygous outcrossing species (Foltz *et al.* 1984). Its mating behaviour has been described by Simroth (1885), Gerhardt (1933, 1934, 1939), Karlin & Bacon (1960), Wiktor (1960), Webb (1961b, 1965), and others. Observations during the present study were consistent with these earlier descriptions. Mating (Fig. 246) is often initiated by directional following by one animal of the freshly laid mucus trail of another. If the pursued animal is receptive, copulation is preceded by a 'courtship dance' during which the animals encircle each other clockwise on an increasingly thick pad of mucus about 75 mm in diameter. This precopulatory behaviour occurs on both vertical and horizontal surfaces in sites above ground where eversion and play of the genitalia are not impeded. Each slug plays its sarcobelum, extended by eversion of the distal phallic region, over the body of its partner as it circles. Gerhardt (1933, 1939) and Webb (1965) correctly stress the importance of the stimulator in courtship. As soon as the stimulators are brought into contact, each slug begins gnawing on the stimulator of the other. This seems to cause or aid reciprocal curvature of the foreparts so as to keep the stimulators in contact.

After about 30 minutes (but as much as 75 minutes) of circling and stimulator gnawing the animals align themselves so as to bring the reproductive openings into opposition. With the animals in rather loose enclaspment, the proximal phallic regions are rapidly and fully everted and then intertwined. The organs are violently rotated back and forth while intertwined and the sarcobela reach their greatest tumescence. Large quantities of clear, viscous seminal material borne on the exterior of the everted phalluses becomes smeared over the phallic structures as they intertwine, thus apparently effecting reciprocal insemination. During this phase of courtship, the phallus flagella are everted and become turgid rods radiated over the united phalluses. Webb (1965) suggested that these flagella function to entangle and anchor the semen so that it becomes engulfed as the phalluses are retracted. Seminal exchange in this species takes only about 30 seconds. Shortly after sperm transfer the slugs separate and crawl off.

As noted by Gerhardt (1939) and Webb (1961b), mature individuals often evince their sexuality by a prominence or dilation of the atrial pore, or by protrusion of the stimulator. Animals in this state are not infrequently observed, in the field and in laboratory cages, to approach conspecifics in an attempt to arouse a mating response.

The eggs, which measure about 3x2.5 mm, are translucent and weakly speckled with calcareous crystals which become absorbed during embryo development. At times eggs are joined together by gelatinous strands, but generally they are deposited lacking this connection. Eggs are generally deposited on the soil surface, under plant litter or other cover.

Remarks. Many authors, especially in the 19th century, did not distinguish between *D. reticulatum* (Müller, 1774) and *D. agrestis* (Linnaeus, 1758), taking them for one species (Luther 1915). In Europe there are, in addition to *D. agrestis*, several species closely related to and resembling *D. reticulatum* (e.g., *D. turcicum* (Simroth, 1894)) but distinguished by characters of the male genitalia.

Several variety names, founded on variations in body coloration, are to be found in the literature (e.g., Quick 1960).

The literature on *D. reticulatum* is very extensive. An introduction into this literature may be obtained from Pilsbry (1948 (1939–48)), van Regteren Altena (1950, 1969), Likharev & Rammel'meier (1952), Quick (1960), Ellis (1967), Bequaert & Miller (1973), Backhuys (1975), Giusti (1976), Wiktor (1973, 1983a, 1989), Likharev & Wiktor (1980), Alonso & Ibáñez (1984), and Alonso *et al.* (1986).

Family ARIONIDAE

Diagnosis. Herbivorous slugs or semi-slugs with a rudimentary shell. Body elongate; mantle small, not covering the entire back. Kidney arched, tending to surround pericardium. Cephalic retractors with a tendency towards division into several individual bands; right ocular retractor muscle either passing over male genitalia or free of genitalia to insert on ocular peduncle. Buccal mass spheroidal. Jaw odontognathic or oxygnathic. Radula with marginal teeth broad, on short basal plates. Intestine forming a single anteriorly directed loop. Genital orifice variously sited on foot, from immediately posterior to right ocular peduncle to visceral stalk below pneumostome. Epiphallus present. Phallus often reduced.

Remarks. The Arionidae as recognised here comprise six subfamilies: Ariolimacinae (Nearctic), Binneyinae (Nearctic), Anadeninae (Nearctic and Oriental), Oopeltinae (southern Africa), Ariopeltinae (southern Africa), and Arioninae (Palearctic). Only Arioninae occur in New Zealand, where they are represented by three naturalised species. Philomycidae (North America and Oriental) are here considered a distinct family, contrary to Tillier (1989), who reduced these slugs to subfamily status within the Arionidae.

Subfamily ARIONINAE

Diagnosis. Mantle small, round, covering about 0.3 of body, containing calcium granules which sometimes form a plate-like rudimentary shell. Pneumostome in anterior right margin of mantle. Back slightly rounded, sometimes with a vestigial keel. Body apex obtuse, with a pit-like caudal cavity just above foot edge. Aulacopod, with well developed foot fringe. Sole undivided. Suprapedal gland embedded in foot tissues. Jaw odontognathic. Kidney arched, its extremities meeting so as to surround pericardium. Genital system with epiphallus well developed or wanting, and phallus greatly reduced or wanting. Free oviduct well developed, often with a ligula. Atrium of varying size and shape, often with lateral pockets. Spermatophores produced in outcrossing species. Genital retractor muscle divided into several small bands, one of them always fixed to bursa copulatrix duct, one to free oviduct, and one usually to atrium. Left and right tentacular retractors arising separately from pallial complex or body wall. Right ocular retractor not passing over male genitalia. Central nervous system with cerebropedal connectives equal in length and rather short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact. Haploid chromosomes number 25–29.

Remarks. Most Arioninae occur naturally in the western Palearctic between the Sahara and the Ural Mountains, but one endemic species is found in Siberia. In the western distribution centre they range north to 68 degrees in Scandinavia, and south to the Sahara, Bulgaria, and southern Ukraine, but are unknown from the Black Sea coast and the Caucasus.

The subfamily includes about 35 species. Because of a rather uniform external and internal body structure in Arioninae it is hard to delimit genera and subgenera. Nevertheless, three groups may be distinguished (Wiktor & Norris 1991), around the following genera. (i) *Arion* d'Audebard de Férussac, 1819 – shell consisting of more or less detached calcium granules; buccal retractor insertion in pallial complex; oviduct, bursa copulatrix duct, and epiphallus opening separately into atrium. (ii) *Geomalacus* Allman, 1843 – slugs with a plate-like shell having concentric growth lines; buccal retractor insertion relatively distant from posterior edge of pallial complex and somewhat on the right side; bursa copulatrix duct and epiphallus opening into a common duct situated on an extension of atrium (termed 'atriopenis') employed during copulation. (iii) *Letourneuxia* Bourguignat, 1866 – slugs with a plate-like shell having concentric growth lines; buccal retractor insertion beyond pallial area but very close to it; epiphallus absent; vas deferens, bursa copulatrix duct and oviduct opening separately into atrium; a large, tongue-like stimulator occupying atrium.

Several species of *Arion* have become widely dispersed throughout the temperate regions of the world through the activities of man.

Genus *Arion* d'Audebard de Férussac

Limax of authors. (Not *Limax* of Linnaeus, 1758, type species *Limax maximus* Linnaeus, 1758, by original designation; Limacidae.)

Arion d'Audebard de Férussac, 1819: 50, type species *Arion empiricorum* d'Audebard de Férussac, 1819 = *Limax ater* Linnaeus, 1758, designated by Fleming (1822) – ICZN Opinion 335 (1955a: 48, 56).

Geomalacus of authors. (Not *Geomalacus* of Allman, 1843, type species *Geomalacus maculosus* Allman, 1843, by monotypy – ICZN Opinion 335 (1955a: 48, 57); Arionidae.)

Lochea Moquin-Tandon, 1855: 10 (as section of *Arion* d'Audebard de Férussac), type species *Arion empricorum* d'Audebard de Férussac, 1819 = *Limax ater* Linnaeus, 1758, designated by Malm (1868).

Prolepis Moquin-Tandon, 1855: 14 (as section of *Arion* d'Audebard de Férussac), type species *Limax subfuscus* Draparnaud, 1805, designated by Malm (1868).

Baudonia Mabille, 1868: 131, type species *Arion timidus* Morelet, 1845 = *Limax ater* Linnaeus, 1758, according to Hesse (1926).

Carinella Mabille, 1870a: 114 (as a subgenus of *Arion* d'Audebard de Férussac), type species *Arion bourguignati* Mabille, 1868 = *Arion circumscriptus* Johnston, 1828, designated by Cockerell (1891c). (Not *Carinella* of Johnston, 1833; Nematomorpha. Not *Carinella* of Sowerby, 1839 (1812–45), in error for *Cancinelle* Adanson, 1757; Mollusca.)

Eugeomalacus Mabille, 1870a: 121 (in part), type species not designated (several species referred to).

Kobeltia Seibert, 1873: 81, type species *Arion hortensis* d'Audebard de Férussac, 1819, designated by Backeljau (1990).

Ariunculus Lessona, 1881: 193, type species *Arion intermedius* Normand, 1852, designated by Kennard & Woodward (1926).

Tetraspis Hagenmüller, 1885: 303, type species *Tetraspis letourneuxi* Hagenmüller, 1885 = *Limax subfuscus* Draparnaud, 1805, by monotypy.

Microarion Hesse, 1926: 66, type species *Arion intermedius* Normand, 1852, by original designation.

Laevigati Mabille, 1870a: 123, for *Geomalacus vendeanus* Letourneux, 1869 and *G. moitessierianus* Mabille, 1867; no type selected but both included taxa are junior synonyms of *Arion intermedius* Normand, 1852.

Diagnosis. Shell internal, represented by separate calcareous granules. Mantle and back usually with lateral bands. Tail wide, obtuse; an indistinct keel present in some juveniles, but never in adults. Mantle shield without concentric ridges. Skin thick. Genital orifice immediately

below pneumostome. Cephalic retractors widely separate at origin from posterior margin of diaphragm. Genital retractor short, arising from diaphragm close to left cephalic retractor, inserted into free oviduct, bursa copulatrix duct, and phallus. Epiphallus strongly developed, rarely with a flagellum. Phallus vestigial, represented by an encompassing tissue ring around verge at entrance into atrium. Genitalia with or without a ligula. Epiphallus/phallus, free oviduct, and bursa copulatrix duct opening into atrium separately. Intestine with a single forward-directed loop, lacking a rectal caecum. Haploid chromosome number 25–29.

Remarks. *Arion* slugs are usually forest dwelling, omnivorous, and have a lifespan of about 1 year. The natural range of the genus is the same as that given for the subfamily. About 25 species are known.

The systematics and taxonomy of *Arion* is problematic owing to a general uniformity in external and internal body structure, and several of the long-established species are in fact a complex of sibling species. Various names have been applied to subgenera and sections of *Arion*, including taxa originally established at generic rank. As the validity and phylogenetic relationships of these infrageneric taxa are not known with any confidence, they are not applied here to New Zealand's naturalised taxa. Taxa originally described at generic level, or subsequently elevated to that status, are here listed under the synonymy of *Arion* d'Audebard de Férussac 1819, the earliest valid generic name for the slugs in question. Several additional names have been applied to sections of genus *Arion*. The reader is referred to Backeljau & de Bruyn (1990) for discussion of infrageneric taxonomy of *Arion*.

Arion distinctus Mabille

Figures 31, 71, 97, 112, 141, 168, 194, 222, C4, M1, M41–44; Map 4

subfuscus of authors (not of Draparnaud, 1805).
? *hortensis* var. *alpha* d'Audebard de Férussac, 1819: 137 (*Arion*).
hortensis of authors (not of d'Audebard de Férussac, 1821).
fuscus of authors (not of Müller, 1774) var. *fasciatus* Moquin-Tandon, 1855: 2 (not of Nilsson, 1823) (*Arion*).
distinctus Mabille, 1868: 137 (*Arion*).
cottianus Pollonera, 1889: 634 (*Arion*).
coerulens Collinge, 1897a: 444 (*Arion*).

Small slug (Fig. 31), extended length of living specimens 25–40 mm. General colour variable, but typically yellowish-grey; on either side of body a longitudinal dark band; head and tentacles blue-black or grey; sole varying from pale yellow to bright orange; body mucus yellow-orange and sticky. Body wall grooved into tubercles. Mantle not grooved into tubercles, but also showing a dark band on either side, this enclosing pneumostome on right side, often with a break or notch immediately dorsal to the orifice.

Shell granules (Fig. M1) discrete, variable in size, located under mantle.

Reproductive system, Fig. 71. Ovotestis grey, often with a reddish or violet tinge in fresh specimens, located in posterior part of body cavity, between lobes of digestive gland. Hermaphrodite duct long and coiled, dilated and folded medially, slender terminally and forming an indistinct talon partially embedded in elongate albumen gland. Spermoviduct long. Free oviduct long and dimorphic, the slender proximal part always terminating in a firm, usually slightly dilated section, the distal part, capable of eversion during copulation, broadening towards atrium, but often lacking. Vas deferens moderately long. Epiphallus short, gradually widening towards vestigial phallus collar and verge at atrium; internal surface with rows of small polygonal papillae; verge a curved plate or low cone penetrated by epiphallial lumen in reaching atrium. Bursa copulatrix reservoir a large sac on a short, wide duct. Genital atrium divided into 2 parts: proximal part with outlets of free oviduct, bursa copulatrix duct, and epiphallus; distal part with genital pore opening to the exterior, a little anterior of pneumostome.

Genitalia provided with 2 retractor muscles, one on distal part of free oviduct and the other on bursa copulatrix duct, inserting on diaphragm beside one another or fused together, behind kidney.

Spermatophore (Fig. 97) markedly elongate and slender (5.0–7.5 mm long by 0.5–0.68 mm in diameter immediately behind collar); anterior end tapering to a straight or slightly curved, blunt nozzle; collar indistinct, partially enclosing spermatophore shaft; an indistinct ridge, sometimes finely serrate, running longitudinally from collar to tapering, blunt, sometimes slightly curved or hooked posterior end.

Jaw (Fig. 112) about 1 mm wide, arcuate, composed of 8–12 fused ridged plates.

Radula (Fig. M41–44) with 100–120 transverse rows of teeth, each with the formula 28–35+C+28–35. Central tooth tricuspid, with a symmetrical basal plate; mesocone elongate, widest medially, terminally pointed; ectocones short and pointed to rounded. Transition from lateral to marginal teeth gradual. First lateral teeth robust, slightly larger than central tooth; external vertex prominent, on wide basal plate; mesocone robust, ovate and pointed; regressed endocone a slight swelling at about 0.4 of mesocone length; ectocone short, wide, and bluntly pointed.

Ectocones diminising in size but increasingly elongate and pointed towards radular margin. Mesocone of outer lateral teeth markedly elongate and pointed. Teeth near margin of radula small, weakly cusped but multicuspid, with the short mesocone most prominent.

Digestive tract, Fig. 141. Buccal mass spheroidal. Oesophagus quickly enlarging to crop. Stomach large, with a prominent posterior gastric caecal sac lying on left, opposite origin of intestine, communicating with digestive gland via 2 openings. Intestine arising from right lateral part of stomach to coil 180 degrees around oesophageal crop before passing over anterior aorta; posterior loop not coiled around crop, extending to 0.7–0.8 of crop length before turning forwards to anus.

Pallial complex (Fig. 168) located more or less in middle of mantle. Heart occupying a central position, with ventricle axis left-inclined, relative to body axis, by about 45 degrees. Aortic stem moderately long, branching after crossing forward intestinal loop. Kidney horseshoe shaped, its extremities meeting above origin of aorta. Primary ureter very short. Secondary ureter long, separating from right anterior border to run to right posterior border of kidney before turning forwards and running to excretory orifice, immediately adjacent to anus. Urinary bladder absent, but ureter frequently saccular in distal part. Pulmonary vessel network anterior, extending a little posteriorly on either side of kidney.

Free muscle system, Fig. 194. Retractor muscles originating in posterior part of pallial complex; buccal retractor arising on body midline and dividing into two muscle bands well before passing throught nerve ring; left and right tentacular retractors arising separately on left and right side respectively; right ocular retractor free of genitalia, inserting on ocular peduncle; genital retractor arising on left, between buccal and tentacular retractors.

Central nervous system, Fig. 222a, b. Cerebral ganglia united by a commissure about equal in length to cerebral ganglion width. Cerebropedal connectives short, their length less than cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal ganglion appressed to right pleural and visceral ganglia; left parietal fused to visceral ganglion, the latter sited to right of median plane.

Chromosome number unknown.

Type material. The type locality of *Arion distinctus* is Sèvres, near Paris. No original material survives (Davies 1979). A neotype (No. alcohol 9 120 in the Rijksmuseum van Naturlijke Historie, Leiden), collected from Sèvres in 1983, was designated by de Winter (1984).

Distribution. Natural range in Europe not known, since *A. distinctus* has only recently been recognised as specifically distinct from *A. hortensis* (Davies 1977, 1979). This species is known to occur through much of Europe (British Isles, Netherlands, Germany, Belgium, Austria, Switzerland, France, Czechoslovakia, Sweden, Norway, Denmark) on the Azores, and in North America and New Zealand.

Recommended common name. Mabille's orange soled slug.

Material examined. New Zealand. AK. Ellerslie, 14 Apr 1987, B.F. Hazelwood and H. Taylor. **WO.** Mangatarata, 6 Jul 1991, B. Wilson; Patetonga, 29 May 1986, S.L. Potter. Ngaruawahia, 17 Oct 1994. Hamilton, 28 Apr 1977, 24 Oct 1977 and 10 Jun 1978. Ohaupo, 4 Jul 1991. Waitomo, 19 Sep 1978. **BP.** Rotorua, Sep 1994, in park. **WI.** Bulls, May 1977, W. Stiefel. **NN.** Motueka, 6 Oct 1994, in grass on dunes. Nelson, 6 Oct 1994, in park. **DN.** Port Chalmers, 16 Feb 1994, in gardens. Dunedin, 15 Feb 1994, on railway siding.

Extralimital. England. Little Witcombe, Gloucestershire, 21 Sep 1990, in oak woodland. Lashford Lane Fen Reserve, Oxfordshire, Sep 1990, in grass. **Netherlands.** Heinkenszand, Zeeland, Oct 1990. **Wales.** Merthyr Tydfil, Mid Glamorgan, May 1990, open woodland.

History in New Zealand. See under *A. hortensis*.

Biology. The biology of *A. distinctus* in New Zealand is poorly known, but observations suggest that reproductive behaviour and phenology are similar to what has been noted for this species in the British Isles by Davies (1977, 1979).

A. distinctus is a cross-fertilising species, and its mating behaviour is similar to that of *A. hortensis*. Copulation lasts no more than 30 minutes (cf. at least 80 minutes in *hortensis*); this shorter time is principally due to the more rapid transfer of spermatophores. Individuals with differing forms of the free oviduct mate freely. The everted oviduct is a broad, rounded, tongue-like structure.

A. distinctus has a lifespan of about 12 months, and is reproductive throughout the period from late winter to early summer. It is more tolerant of extreme winter and summer conditions than *A. hortensis*, and therefore tends to be reproductive all year round in many localities.

Common in disturbed habitats, *A. distinctus* is easily found under stones, pieces of wood, and crowns of tussock-forming grasses. It is a pest in vegetables.

Remarks. Davies (1977, 1979) and others have shown that *A. distinctus* is part of a complex of three sibling species including *A. hortensis* d'Audebard de Férussac,

1819 s.s. (q.v.) and *A. owenii* Davies, 1979. In an earlier revision of New Zealand's naturalised slugs (Barker 1979) only *A. hortensis* s.s. of this complex was recognised as being present. A re-examination of the material studied by Barker (1979) and further collecting have revealed the presence in New Zealand of both *A. hortensis* s.s. and *A. distinctus*.

Since *A. hortensis* and *A. distinctus* show much variation in both general colour and banding pattern, their separation on the basis only of external appearance is always doubtful. For example, besides the typical blue-black *A. hortensis* with more dorsal mantle bands there are also paler forms with mantle bands situated more ventrally. On the other hand dark forms of *A. distinctus* exist with mantle bands enclosing a rather narrow, pale-coloured dorsal field. In a sample of a mixed population (sympatry occurs in New Zealand) it is possible to distinguish the species, since *A. hortensis* always appear darker, with more dorsally situated mantle bands, in comparison with the paler *A. distinctus*. The latter species always lacks any reddish or violet tinge in the head and ocular peduncles, often present in *A. hortensis*.

The only character by which *A. distinctus* and *A. hortensis* s.s. are reliably distinguished is the structure around the outlet of the epiphallus: in the former, verge a curved plate or low cone penetrated by the epiphallus lumen; in the latter, verge an oblong plate partially overhanging but not penetrated by the epiphallus lumen. The free oviduct in *A. hortensis* s.s. is always tripartite, while that of *A. distinctus* may be tripartite, or bipartite with the eversible part lacking (Davies 1977, Backeljau & de Bruyn, 1990). Both forms of oviduct are apparent in the New Zealand material of *A. distinctus*.

Several variety names, founded on variations in body coloration, are to be found in the literature (e.g., Hesse 1926, Quick 1949).

An introduction into the literature on *A. distinctus* is provided by Davies (1977, 1979), de Wilde (1983), Backeljau (1985a), Backeljau & Marquet (1985), Backeljau & van Beeck (1986), Dolan & Fleming (1988), Backeljau & de Bruyn (1990), and Vater (1991).

Arion hortensis d'Audebard de Férussac

Figures 32, 72, 98, 113, 142, 247, C5, M45–47; Map 5

fuscus of authors (not of Müller, 1774).
subfuscus of authors (not of Draparnaud, 1805).
hortensis d'Audebard de Férussac, 1819: 65 (*Arion*).
? *fuscus* (not of Müller, 1774) var. *limbatus* Moquin-Tandon, 1855: 14 (*Arion*).
fuscus (not of Müller, 1774) var. *pyrenaicus* Moquin-Tandon,

1855: 14 (*Arion*).
? *pelophilus* Mabille, 1870a: 117 (*Arion*).
? *incommodus* Hutton, 1879: 331 (*Arion*).
? *fallax* Sterki, 1882: 150 (*Arion*).
elongatus Collinge, 1894: 66 (*Arion*).
? *rubellus* Sterki, 1911: 64 (*Arion*).

Small slug (Fig. 32), extended length of living specimens 25–50 mm. General colour variable, but in typical forms blue-black with a nearly black dorsum; on either side of body a longitudinal dark band; head, ocular peduncles, and inferior tentacles with a reddish or violet tinge; sole varying from pale yellow to bright orange; mucus yellow-orange and sticky. Bodywall grooved into tubercles. Mantle not grooved into tubercles, but also showing a dark band on either side, situated rather dorsally; right mantle band running over pneumostome, never showing a break or a notch.

Shell granules discrete, variable in size and distribution under mantle.

Reproductive system, Fig. 72. Ovotestis grey (often with a reddish or violet tinge in fresh specimens), located in posterior part of body cavity, between lobes of digestive gland. Hermaphrodite duct long and coiled, dilated and folded medially, slender terminally, forming an indistinct talon partially embedded in elongate albumen gland. Spermoviduct long. Free oviduct long, proximally slender, medially firm and slightly dilated, and with a long distal region, eversible as a slender process during copulation, broadening towards atrium. Vas deferens short. Epiphallus of similar length to vas deferens, enlarging gradually in width towards vestigial phallus collar and verge at atrium, internally with rows of small polygonal papillae; verge an inconspicuous oblong plate, initimately associated with and partially overhanging epiphallus outlet. Bursa copulatrix reservoir a large, rounded sac on a short, wide duct. Genital atrium divided into 2 parts: proximal part with outlets of oviduct, bursa copulatrix duct, and epiphallus; distal part with genital pore opening to the exterior, a little anteriad of the pneumostome.

Genitalia provided with 2 retractor muscles, one on distal part of firm portion of free oviduct, the other on duct of bursa copulatrix; retractors inserted on diaphragm beside one another or fused together, behind kidney.

Spermatophore (Fig. 98) short and relatively stout (4.5–5.2 mm long, 0.95–1.05 mm diameter immediately behind collar); anterior (apical) nozzle short, sharply pointed, and deflected up to 90 degrees from longitudinal axis; a distinct serrated ridge with about 25 barbs per mm oriented towards apical end, rotating up to 90 degrees along shaft from collar to bluntly tapered and strongly hooked posterior end.

Jaw (Fig. 113) about 1 mm wide, arcuate, composed of

7–12 fused ridged plates.

Radula (Fig. M45–47) with 100–120 transverse rows of teeth, each with the formula 29–35+C+29–35. Central tooth tricuspid, with a wide symmetrical basal plate; meso-cone slender and pointed; ectocones short and pointed to rounded. Transition from lateral to marginal teeth gradual. First lateral teeth robust, with only the external vertex pro-minent on a wide basal plate; mesocone long and robust, pointed; regressed endocone a slight indentation at about 0.5 of mesocone length; ectocone short, wide, and sharply pointed. Teeth near margin of radular ribbon small, weakly cusped but multicuspid, with the short mesocone most prominent.

Digestive tract, Fig. 142. Buccal mass spheroidal. Oes-ophagus quickly broading to large crop. Stomach large, communicating with digestive gland via 2 openings; post-erior gastric caecal sac prominent, lying on left opposite origin of intestine. Intestine arising from right lateral part of stomach and coiling 180 degrees around oesophageal crop before passing over anterior aorta; posterior loop not coiled around crop, extending to only 0.6–0.8 of crop length before turning forwards to anus.

Pallial organs, retractor muscles, and central nervous system essentially as in *A. distinctus*.

Haploid chromosome number 28.

Type material. D'Audebard de Férussac's original material, labelled "montagnes env. de Clermont (Oise)" (France), is in the Muséum National d'Histoire Naturelle, Paris (Davies 1979); lectotypic designations have been made by de Winter (1984). This material was not exam-ined during the present study.

Distribution. The limits of *A. hortensis* s.s. in Europe are not known, as most records refer to the species complex of *A. distinctus*, *A. owenii*, and *A. hortensis* (see above). *A. hortensis* is recognised in Belgium, England, Wales, the Netherlands, France, Germany, and Switzerland, and as introductions in the U.S.A. and New Zealand.

Recommended common name. Férussac's orange soled slug.

Material examined. New Zealand. ND. Whangarei, 3 May 1993, H.I. Thomsen. **AK**. Leigh, Dec 1979, R. Willan. Kaipara Flats, 22 Jan 1989, A.S. McBride. Browns Bay, 16 Sep 1991, in gardens. Auckland, 1891, Musson (AMSA, Musson collection C.108533). Mt Albert, 27 May 1976, N.A. Martin. Glen Eden, Nov 1977, G.W. Ramsay. Titirangi, 18 Sep 1974, N.A. Martin; 27 Oct 1977, G.W. Ramsay; 29 Oct 1977, J.A. Ramsay. Ellerslie, 14 Apr 1987, B.F. Hazelwood & H. Taylor. Pukekohe, 26 May 1976 and 2 Nov 1976, N.A. Martin. **CL**. Flaxmill Bay, 20 Feb 1978. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in

coastal forest, 15 m alt. Thames, Oct 1988, in park lawn. **WO**. Mangatarata, 6 Jul 1991, B. Wilson. Tahuna, 25 May 1976 and 26 May 1977, in maize stubble. Waingaro, Sep 1993, at roadside. Orini, 11 Dec 1980, gardens. Matamata, 4 May 1992, in gardens. Te Poi, 2 Jul 1977. Hinuera, 8 Jan 1993, in *Podocarpus dacrydioides* forest remnant. Matangi, 18 Jul 1980, R.N. Watson, in commercial asparagus stand. Matangi, Whewell's Bush, 14 Jan 1996, in *Podocarpus dacrydioides* forest remnant. Hamilton, 7 Mar 1976, 3 Sep 1976, 7 Jan 1977, 21 Aug 1977, and 24 Sep 1978. Te Miro, 19 Apr 1977. Te Kowhai, 19 Sep 1978. Raglan, 3 Nov 1994, in grassy area on coastal cliff; 13 Nov 1994, H. Oliver, aestivating at 15 cm depth in pasture soil. Te Uku, 12 Jul 1977. Rukuhia, 18 Oct 1989, in pasture. Ohaupo, 4 Jul 1991. Karapiro, Aug 1980, R.N. Watson, in asparagus. Mt Kakepuku, 15 Jan 1977, in grass clearing at summit. Putaruru, 6 Sep 1994, T.J. Patterson, in garden. Waitomo, 22 Jun 1976 and 19 Sep 1978. Oparure, 19 Dec 1977. **BP**. Rotoma, 29 May 1977. Whakatane, 21 Jan 1980, H. Hines. Torere, Oct 1988, in grassy area at roadside. Raukokore, 15 Sep 1992, in coastal *Beilschmiedia tawaroa-Vitex lucens* forest. Hicks Bay, 17 Nov 1977. Mamaku, 25 Jan 1996, in broadleaf scrub. Tarawera, Jan 1980, in grassy areas at roadside and in *Leptospermum* scrub. **GB**. Gisborne, 3 Nov 1978, N. Harding; 12 Nov 1996, J. Hurrell, in *Pisum sativum* crop. **TO**. Whakamaru, 7 Jul 1978. Aratiatia, Dec 1995, in broadleaf scrub. **TK**. New Plymouth, 30 Jan 1989, J. Hanna. **WI**. Bulls, May 1977, W. Stiefel. **WN**. Wellington, 17 Feb 1994, in garden. **SD**. Picton, 12 Mar 1991, A.A. Blair. **NN**. Nelson, 1 Jul 1978, J. Marris. Mapua, 29 Nov. 1977, L. & M. Collage; 24 Apr 1978, W.K. Marris. Richmond, 19 Dec 1977, R. Marr. Aniseed Valley, 15 Jul 1978, C.C. Meikle. **MB**. Blenheim, 28 May 1988, W.Y. Fords. **MC**. Christchurch, 24 Nov 1990, J. Witten. **BR**. Westport, 1 Oct 1989, N.T. Whitney. Greymouth, 14 Dec 1993, D.L. Lane. **DN**. Dunedin, undated (BMNH, *Arion incommodus* Hutton, ex Otago Museum, type?). Port Chalmers, 16 Feb 1994, in gardens. Portobello, 16 Feb 1994, in grassy area of coastal bank. Mosgiel, Mar 1982, T.G. Watson.

Extralimital. England. Cowleace National Reserve, Oxfordshire, 27 Oct 1990, in beech woodland. **Ireland**. Oughterard, Galway, 26 Aug 1990, in rock wall; Killarney, Kerry, 24 Aug 1990. **Netherlands**. Heinkenszand, Zeeland, Oct 1990. **Poland**. Cieszyn, 11 Sep 1960, coll. & det. A. Wiktor. **Scotland**. Auchincruide, Dumfries & Galloway, Sep 1990, in woodland. **Wales**. Devil's Bridge, Dyfed, 21 Sep 1990, in oak woodland.

History in New Zealand. *A. hortensis* s.l. was first recorded in New Zealand by Hutton (1879). Not recog-nising the naturalised status of his Dunedin material, Hutton described a new species under the name *Arion incommodus*. Subsequently Hutton (1880, 1881, 1883) provided descriptions of the anatomy and, in the latter papers, reduced his species to synonymy under the European *Arion fuscus* Müller, 1774 (= *Arion subfuscus* Draparnaud, 1805). This assignment of the Dunedin material to *A. fuscus* was followed by Simroth (1889b) and Musson (1891), and thus *A. subfuscus* was established in the malacological literature as an element of the natural-

ised fauna of New Zealand (e.g., Powell 1979). The absence of *A. subfuscus* from the New Zealand fauna and the assignment of Hutton's *A. incommodus* to the *A. hortensis* complex was established by Barker (1979). The correct position of *A. incommodus* within the *A. hortensis* complex, however, remains problematic (see Remarks).

The presence of *A. hortensis* s.l. was first recognised by Musson (1891), who had collected material from Auckland. Taylor (1902–07 (1902–21)) states that this record was in error, Musson's material being referable to *A. intermedius* Normand, 1852. Musson's material, in AMSA, has been examined (Barker 1979) and found to be conspecific with *A. hortensis*. Thomson (1922) gives Taranaki as a further locality for *A. hortensis* and Quick (1952) lists Dunedin, but the source of his information was not given. From collections made in the 1950s, Whitten (1955) recorded *A. hortensis* from the Thames district.

Quick (1960) mentions neither *A. subfuscus* nor *A. hortensis* as occurring in New Zealand but lists *A. intermedius*, apparently modifying his earlier references to New Zealand (Quick 1949, 1952) to follow Taylor (1902–07 (1902–21)). Powell (1979) provided no new information on *Arion* in New Zealand, merely repeating the records given in Suter (1913).

Thus, for the century that followed Hutton's (1879) initial record, the malacological literature relating to *A. hortensis* s.l. was confused as to nomenclature. Further, the scarcity of records indicated a very limited distribution.

Barker (1979) found *A. hortensis* s.s. to be widespread and common in the North Island, but for the South Island had records only from Nelson and Dunedin, the latter based solely on the type locality for *A. incommodus*. Following further extensive collecting, Barker (1982) concluded that *A. hortensis* was found throughout the North and South islands, but less commonly in the southern South Island. Additional collecting over the past decade has confirmed that spatial pattern for *A. hortensis* s.s. However, *A. distinctus* is now recognised as being present at widely scattered localities in both North and South islands, often sympatrically with *A. hortensis*.

It is thus probable that both *A. hortensis* and *A. distinctus* have long been resident and widespread in New Zealand.

Biology. *A. hortensis* breeds by cross-fertilisation (Backeljau & de Bruyn 1990). Mating behaviour (Fig. 247) observed in New Zealand populations agrees closely with descriptions by Davies (1977, 1979) for this species in the British Isles. A sexually active slug may follow, and nibble, members of other *Arion* species or its conspecifics before finding a receptive partner. The mating pair en-

circle each other and settle before the genitalia are everted and joined. The everted oviduct is finger-like and mobile, and is withdrawn and everted several times and played over the partner's back during coitus. A period of 30–60 minutes elapses before spermatophores are exchanged. As the genitalia are retracted after mating, the received spermatophore becomes lodged in the atrium, with its collar region attached at the opening of the bursa copulatrix duct. Davies (1987) remarked that, during transfer, spermatophores are covered with a thick mucus.

These slugs are basically annual. Under New Zealand conditions breeding occurs 6–8 months after hatching, and sexual maturity generally is reached in autumn. Eggs measuring 2×2.5 mm and milky white from the calcite crystals suspended in their jelly capsule are produced in clutches of 10–50 throughout the period from autumn to late spring. Growth and breeding are generally arrested by dry summer conditions. In times of dry soil conditions, *A. hortensis* aestivates under logs and stones in cells fashioned from body mucus and soil.

A. hortensis is common in a wide range of disturbed habitats, including gardens, arable crops, roadsides, forest fringes, and grassy tracks in forest, but is less common in pastures. The slugs are easily found under stones, pieces of wood, and crowns of tussock-forming grasses. *A. hortensis* feeds extensively on fungi and decaying leaf material, but in cultivated areas is frequently a pest in vegetables.

Remarks. Until recently a complex of three species has been confused under the name *Arion hortensis* (Davies 1977, 1979) (see above under *A. distinctus*).

The correct assignment of *A. incommodus* Hutton, 1879 remains uncertain. Barker (1979) tentatively listed it as a synonym of *A. hortensis* s.s. A specimen in BMNH, which is probably Hutton's holotype, is in external appearance attributable to any one of the three species in the *A. hortensis* complex, while the genitalia are similar to the condition in *A. owenii* Davies, 1979. Topotypic material collected to date from Dunedin includes both *A. distinctus* and *A. hortensis* s.s.

De Winter (1986) comments on the possibility of *Arion anthracius* Bourguignat, 1866 being a valid species.

Various variety names, based on variations of body coloration and markings, are to be found in the literature (e.g., Taylor 1902–07 (1902–21), Hesse 1926, Quick 1949, 1960).

An introduction into the literature pertaining to *A. hortensis* is provided by Davies (1977, 1979), Likharev & Wiktor (1980), de Wilde (1983, 1986), Wiktor (1983a), Backeljau (1985a), Backeljau & Marquet (1985), Backeljau & van Beeck (1986), Dolan & Fleming (1988), and Backeljau & de Bruyn (1990).

Arion intermedius Normand

Figures 33, 73, 99, 114, 143, 169, 195, 223, C6, C7, M2, M48–50; Map 6

flavus Müller, 1774: 10 (not of Linnaeus, 1758) (*Limax*).
fuscus of authors (not of Müller, 1774).
hortensis of authors (not of d'Audebard de Férussac, 1819).
fuscatus Morelet, 1845: 32 (not of d'Audebard de Férussac, 1819) (*Arion*).
intermedius Normand, 1852: 7 (*Arion*).
bourguignati Mabille, 1867: 58 (*Geomalacus*).
? *paladilhianus* Mabille, 1867: 60 (*Geomalacus*).
? *moitessierianus* Mabille, 1867: 61 (*Geomalacus*).
hiemalis Drouët, 1867: 59 (*Geomalacus*).
mabillei Baudon, 1868: 142 (*Geomalacus*).
pascalianus of authors (not of Mabille, 1868).
vendeanus Letourneux, 1869: 51 (*Geomalacus*).
verrucosus Brevière, 1881: 310 (*Arion*).
mabillianus Baudon, 1884: 200 (not of Bourguignat, 1866 (1863–70)) (*Arion*).
minimus Simroth, 1885: 237 (*Arion*).
intermedius var. *apennina* Pollonera, 1889: figs 11, 12 (*Arion*).
mollerii Pollonera, 1889: 639 (*Arion*).
vejdovskyi Babor & Kostál, 1893: 1 (*Arion*).
hessei Simroth, 1894: 295 (*Arion*).
obesoductus Reischütz, 1973: 229 (*Arion (Microarion)*).

Small slug (Fig. 33) 10–25 mm in extended length when mature. General coloration variably greyish- or greenish-yellow or yellowish-white, with head and tentacles often darker; usually on either side of body a longitudinal dark band; sole yellowish-grey; mucus yellow. Body wall grooved into tubercles which, when raised in the contracted live animal, have a serrated ridge. Mantle not grooved into tubercles but also usually showing a dark band on either side; bands often united along posterior mantle margin to form a lyre-like pattern.

Shell granules (Fig. M2) minute, sometimes aggregated into an irregular mass, located under mantle.

Reproductive system, Fig. 73. Ovotestis deeply pigmented, lying between lobes of digestive gland, partly exposed dorsally. Hermaphrodite duct long, weakly contorted and dilated in medial section, narrowing towards its termination with an indistinct talon partially embedded in linguiform albumen gland. Spermoviduct moderately short but voluminous. Free oviduct and vagina very short and stout, lacking internal ligula-like structures. Vas deferens slender, about 1.5× length of combined free oviduct and vagina, thin-walled with some folds on inner surface. Epiphallus rapidly broadening towards atrium, terminating in a pronounced vestigial phallus collar; inner surface with rows of small polygonal papillae; verge a vestigial, papillate fold, forming a raised rim about the epiphallus entrance into atrium. Bursa copulatrix reservoir large and spheroidal; duct very short, stout, its distal part with a ring-shaped thickening from which, on side facing epiphallus, a tongue-like structure protrudes slightly into genital atrium. Atrium elongate, with bursa copulatrix duct, epiphallus, and vagina opening close together in proximal part; walls glandular. Genital orifice immediately below pneumostome.

Genital retractor system comprising many small muscles. A large muscle arising from body wall near left margin of diaphragm, distally divided to send one branch to vestigial phallus on distal part of epiphallus and adjacent vagina and another to spermathecal duct. A slender accessory retractor arising from body wall near anterior margin of pallial complex and ending in wall of vestigial phallus, facing vagina. Another slender muscle arising in body wall near genital orifice and ending where phallus collar attaches to proximal atrium.

Spermatophore (Fig. 99) 3–3.8 mm in length; anterior nozzle about 0.6 mm in length, conical, with sharply pointed apex; body elongate, widest medially, often with an ill-defined serrate longitudinal crest, particularly at anterior end.

Jaw (Fig. 114) about 1 mm wide, composed of 7–15 fused plates.

Radula (Fig. M48–50) with 95–120 transverse rows of teeth, each with the formula 28–35+C+28–35. Central tooth tricuspid, with a wide symmetrical basal plate; mesocone long, slender and pointed; ectocones short (about half length of mesocone) and pointed. First lateral teeth robust, with only external vertex prominent on wide basal plate; mesocone long and robust; endocone regressed, a slight indentation at about 0.6 of mesocone length; ectocone short but wide and sharp. Basal plate gradually reducing in height, and mesocones and ectocones in size, with more lateral placement of teeth on radular ribbon, with a gradual transition from lateral to marginal teeth. Teeth near extreme lateral margins distinguished by their marked reduction in size, short, bluntly pointed mesocone, and endocone broken into several small points.

Digestive tract, Fig. 143. Buccal mass spheroidal. Oesophagus quickly enlarging to crop. Stomach large, communicating with digestive gland via 2 openings; posterior gastric caecal sac absent or small. Intestine issuing from right side of stomach and coiling 180 degrees around oesophageal crop before passing over anterior aorta; posterior loop not coiled around crop, extending nearly to level of stomach, before running forwards to anus.

Pallial complex (Fig. 169) located in middle of mantle, with heart occupying a central position; ventricle axis left-inclined by 45 degrees relative to body axis. Aortic stem short, branching as it crosses forward intestinal loop. Kidney horseshoe-shaped, its extremities meeting above

origin of aorta. Primary ureter very short. Secondary ureter long, separating from right anterior border of kidney to run to right posterior border before turning forwards and running to excretory orifice immediately adjacent to anus. Urinary bladder absent, but ureter frequently saccular in distal part. Pulmonary vascular network not well developed, largely confined to area anterior to kidney.

Free muscle system, Fig. 195. Buccal retractor arising at posterior margin of diaphragm, on or slightly to left of body midline. Left and right tentacular retractors arising separately at left and right posterior margins of pallial complex; right tentacular retractor arising a little forward of origin of left retractor; right ocular retractor not crossing over genitalia, inserting on ocular peduncle.

Central nervous system, Fig. 223. Cerebral ganglia united by a commissure about equal in length to cerebral ganglion width. Cerebropedal connectives short, their length less than cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal ganglion appressed to right pleural and visceral ganglia; left parietal fused to visceral ganglion, the latter sited to right of median plane.

Haploid chromosome number 28.

Type material. The type locality is "environs de Valenciennes", France. The whereabouts of the type material is unknown, and it is presumed lost.

Distribution. *A. intermedius* is naturally distributed throughout central and western Europe, and has been introduced passively into South Africa, North America, Australia, and New Zealand.

Recommended common name. Glade slug.

Material examined. New Zealand. ND. Whau Bay stack, 21 Apr 1993, R. Parrish. Paihia, 11 Aug 1974, M.A. Cumber. Rangi Point, Jan 1991. Kohukohu, Jan 1991, in grass at forest edge. Horeke, Jan 1991. Waipoua State Forest, Jan 1992, in grassy area at roadside. Kaitui State Forest, 4 May 1993, R. Parrish. Otakairangi, 1 Nov 1978, in pasture. Matarau, 13 Nov 1986, G.M. Barker & L.N. Robertson, in pasture. Brynderwyn Hills, 25 May 1993, R. Parrish. **AK.** Te Hana, 23 Feb 1994, in pasture. Okaka, 21 Oct 1978. Otakinini, 21 Oct 1978, in pasture. Rangitoto I., 5 Jan 1993, in forest. Titirangi, 29 Oct 1978, A.W. Ramsay. Glen Eden, Nov 1993, G.W. Ramsay. Whakatiwai, 30 Jan 1993. Patumahoe, 5 Jun 1989, in pasture. Mangatawhiri, 11 Jul 1990, in pasture. Maramarua, 11 Jul 1990, in pasture. Waitakaruru, 3 May 1988, in pasture and grassy river bank. **CL.** Coroglen, 12 Jan 1996, in *Leptospermum* scrub and pasture. Puketui, 9 Jan 1996, in pasture. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. Thames, 15 Dec 1979, in grassy area on coastal bank. Whangamata, Jan 1993. Waihi, Jan 1993, in scrub. **WO.** Port Waikato, Mar 1987, in

dunes and pasture. Onewhero, Mar 1987, in grassy area at roadside. Limestone Downs, Mar 1987, in pasture. Tahuna, 26 May 1977, in maize stubble. Tauwhare, 15 Dec 1994, in pasture. Ohinewai, 18 Jul 1977, in pasture. Waikaretu, Mar 1987, in pasture. Waingaro, 8 Sep 1993, in pasture and scrub. Whangamarino Swamp, 7 Feb 1988, in grassy bank. Tirohia, Aug 1993, in pasture. Hinuera, Dec 1992, in pasture and *Podocarpus dacrydioides* forest; 8 Jan 1993, in *Podocarpus dacrydioides* forest remnant. Tauwhare, 22 Feb 1995, in pasture. Matangi, Whewell's Bush, 14 Jan 1996, in *Podocarpus dacrydioides* forest remnant. Hamilton, 7 Mar 1976, in gardens. Rukuhia, 20 Jul 1978, in pasture. Matangi, 8 Sep 1975, N.A. Martin; 20 Feb 1979. Matangi, 18 Jul 1980, R.N. Watson, in commercial asparagus. Te Miro, 19 Apr 1977. Whatawhata, 21 Dec 1993 and 3 Jan 1994, in pasture on limestone. Glen Massey, Aug 1994, in pasture. Raglan, 10 Sep 1977. Ruapuke, 27 Jan 1996, in coastal broadleaf forest. Ohaupo, 8 Nov 1992 and 8 Mar 1994, in pasture. Ohaupo, 8 Nov 1992, in *Podocarpus dacrydioides* forest remnant. Mt Karioi, 6 Jun 1976, in pasture and *Leptospermum* scrub. Ngaroto, 7 Nov 1992, in pasture. Pirongia, 19 Sep 1978, in grassy area at roadside. Karapiro, Mar 1992, in pasture. Lichfield, Apr 1987, in pasture. Honikiwi, Sep 1980, in pasture. Maihihi, May 1987, in pasture. Waipapa, Jun 1980, in *Leptospermum* scrub. Waitomo, Feb 1993, in pasture and forest edge. Oparure, 11 Sep 1976, 19 Dec 1977, 22 Jun 1978, and 21 Sep 1978, in pasture. Rangitoto, 14 Apr 1977, in pasture. Mairoa, Aug 1977, in pasture. **BP.** Athenree, Jan 1993, in pasture. Kaimai Range, nr Katikati, Jan 1994, in forest clearing. Lower Kaimai, 5 Jun 1977, 27 Dec 1977 and 9 Sep 1978, in pasture and *Pinus* plantation. Ohauiti, Mar 1988, in pasture. Te Puke, 6 Jul 1989, C. Marshall, in pasture. Mamaku Forest, 31 Jan 1977, in grassy areas of forest tracks. Mamaku, 25 Jan 1996, in broadleaf scrub. Okataina, 19 Dec 1976, in secondary forest. Manawahe, 18 Dec 1976, 29 May 1976 and 29 May 1977, in pasture and forest. Whangaparaoa, 14 Sep 1992, G.M. Barker & P.C. Mayhill. Raukokore, 15 Sep 1992, in disturbed coastal *Beilschmiedia tawaroa-Vitex lucens* forest. Potaka, 16 Sep 1992, in *Beilschmiedia tawa* forest. Hicks Bay, 20 Sep 1992, in pasture. Oponae, Oct 1988, in pasture. **TO.** Reporoa, 4 Mar 1994, in pasture. Pureora, 16 Dec 1991, in pasture and *Melicytus-Leptospermum* scrub. Aratiatia, 25 Jan 1996, in broadleaf scrub. National Park, Mahuia Camp, 24 Apr 1978, in scrub. **GB.** Waioroho, 17 Sep 1992, in pasture and open *Podocarpus dacrydioides* forest. Te Araroa, 21 Sep 1992, in grassy areas of gravel dunes. East Cape, 20 Sep 1992, in coastal forest and scrub. Rangiata, 20 Sep 1992, in disturbed coastal forest. Tapuwaeroa, Oct 1988, in *Leptospermum* scrub. Te Karaka, Jun 1981, in pasture and maize stubble. Waihirere, 21 Jun 1978, A.C. Firth. Whangara Valley, 16 Dec 1977, in pasture. **TK.** Inglewood, Sep 1991, in pasture. Stratford, Sep 1991, in grass area at roadside. **RI.** Taihape, Dec 1990, in pasture. **WI.** Whangaehu Valley, Mar 1977, G. Crouchley, in pasture. **WA.** Blairlogie, 27 May 1977, G. Crouchley, in pasture. Masterton, 27 May 1977, G. Crouchley, in pasture. **WN.** Upper Hutt, 15 May 1991, in *Beilschmiedia tawa* forest. Cape Terawhiti, Mar 1980, in pasture. Wellington, Sep 1994, in park. **NN.** Parapara Inlet, 30 Jul 1978, C.C. Meikle. Wakefield, 6 Oct 1994, in pasture and disturbed *Podocarpus dacrydioides* forest. **BR.** Westport, 24 Nov 1993, H. Vincent.

KA. Lyndon, Dec 1991, F.J. Rose. WD. Otira, May 1990, H. White. MC. Riccarton, Christchurch, 18 May 1990, in grassy forest clearing. Halswell, Nov 1976, R.H. Blank, in pasture. Ashburton, 4 Apr 1977, J. Wood. OL. Mt Nicholas Station, 30 Apr 1989, E. Nelson. CO. Miller's Flat, Aug 1977, B.I.P. Barratt, in oversown tussock grassland. Rocklands, Sep 1982, B.I.P. Barratt & G.M. Barker, in oversown tussock grassland. DN. Flagstaff, 16 Feb 1994, in grassy area in *Pinus* plantation. Mosgiel, 15 Feb 1994, in pasture. SL. Waimatua, 12 Aug 1993, G.G. Smith, in pasture. SI. Halfmoon Bay, Jan 1979, P.C. Mayhill. Chatham Is. Pitt I., 30 Sep 1976, in pasture and open forest. Auckland Is. Auckland I., Dec. 1983, P.C. Mayhill.

Extralimital. England. Bowsey Hill, Berkshire, 28 Apr 1990, in oak woodland. Ireland. Glengarriff, Cork, 24 Aug 1990, in coastal woods. Poland. Koszalin, 30 Jul 1965, coll. & det. A. Wiktor.

History in New Zealand. Taylor (1902–07 (1902–21)) refers the Auckland record of *A. hortensis* by Musson (1891) to this species, as he does for Hutton's (1879) *A. incommodus* from Dunedin. Musson's material belongs to *A. hortensis* s.s., while Hutton's *A. incommodus* belongs to the *A. hortensis* complex. Taylor (1902–07 (1902–21)) also gives Manapouri (SL) and Paradise (OL) as localities for *A. intermedius*, following reports by W.D. Roebuck in 1905 of this species in gardens.

Longstaff (1912) wrote of Mrs Longstaff finding specimens of *A. intermedius* on Rangitoto Island and at Matahiwi near Masterton in 1910. These records suggest that *A. intermedius* was well established and of widespread occurrence in New Zealand by the early 20th century. Longstaff's two records were repeated in the literature, as *A. minimus*, by Suter (1913), Thomson (1922), Whitten (1955), Coleman (1970), and Powell (1979). Only Whitten (1955) added new information, with confirmation of *A. intermedius* on Rangitoto.

Barker (1979, 1982) confirmed the widespread occurrence of *A. intermedius* in New Zealand, including offshore islands.

Biology. *A. intermedius* apparently has a predominantly uniparental, probably autogamic, breeding system (see Remarks). It is most abundant in relatively undisturbed areas, and as such is a characteristic element in the faunas of woodland and ecotonal habitats. In New Zealand it can be locally abundant in pastures, but is most frequently encountered in hedgerows, scrubland, plantation forests, and native forest areas. Slugs of this species are encountered often in forest and scrub areas disturbed by man's activities such as mining and logging, and from these areas frequently penetrates several kilometres into dense, relatively undisturbed native forest and subalpine scrubland.

The reproductive and population biology of *A. inter-medius* in North Island hill country pastures has been studied by Barker (1991a). In that environment it has an annual life cycle. Eggs are ellipsoidal, about 2 mm in greater diameter, and opaque because of numerous calcite crystals in the jelly layers. Eggs laid during late summer and autumn hatch during autumn and winter.

A. intermedius is a more hardy animal than the other *Arion* species. It may not achieve pest status, and tends to be dispersed whereas the other species are gregarious, but it is more successful on lighter and less hospitable soils, where it is often the only species of this group present. *A. intermedius* is active for most of the year, even during the coldest months, and has the ability to aestivate during dry periods in cells constructed of mucus, soil, and moss.

Remarks. Mating has never been observed in *A. intermedius*, and eggs of individuals raised in isolation have been shown to be viable (Davies 1977). Genetic variation studies based on enzyme electrophoresis demonstate the constant homozygosis of many different populations (McCracken & Selander 1980, Foltz *et al.* 1982a). *A. intermedius* may therefore consist of monogenic strains resulting from an automictic mode of reproduction, probably self-fertilisation (McCracken & Selander 1980, Foltz *et al.* 1982a, 1984, Backeljau 1985a, Backeljau & de Winter 1987, Backeljau *et al.* 1987, Backeljau & de Bruyn 1990, Backeljau *et al.* 1992). It is at present not possible to determine the systematic rank of these strains -- whether separately or collectively they constitute true biological species. Reischütz (1973) assigned specific status (*A. obesoductus*) to one such strain. The presence of spermatophores in the bursa copulatrix of some individuals (Garrido *et al.* 1995, this study) indicates the possibility of a mixed breeding system in *A. intermedius*.

Various varietal names, founded on variations in body coloration and markings, are to be found in the literature (e.g., Taylor 1902–07 (1902–21), Hesse 1926, Quick 1949, 1960).

Introduction to the extensive literature on *A. intermedius* is provided by Germain (1930), Pilsbry (1948 (1939–48)), Likharev & Rammel'meier (1952), Quick (1960), Wiktor (1973), Riedel & Wiktor (1974), Backhuys (1975), Davies (1977), Likharev & Wiktor (1980), Backeljau (1985a, b), Backeljau & van Beeck (1986), Dolan & Fleming (1988), Manganelli & Giusti (1988), Backeljau & de Bruyn (1990), and Backeljau *et al.* (1992).

Family COCHLICOPIDAE

Diagnosis. Herbivorous snails. Shell elongate, under 10 mm in height, imperforate, glossy, subtranslucent, capable of housing retracted animal; aperture ovate, longer than wide, sometimes armed with barriers; lip not expanded, but thickened within; columella slightly sinuate to truncate at base. Sole holopod, undivided or indistinctly tripartite. Foot without a caudal mucus pit. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw aulacognathic. Radula with marginal teeth short, broad, multicuspid. Intestine with a single loop directed forwards. Kidney very long, divided internally into 2 distinct regions, the anterior region functioning as a primary ureter; some taxa with a closed secondary ureter extending to top of pulmonary cavity. Columellar muscle dividing a short distance from its origin into left and right cephalic retrac-tor bundles; buccal retractor associated with left branch, tail fan associated with right branch. Right ocular retractor crossing phallus. Phallus retractor arising from diaphragm, unbranched. Genital orifice at about 0.3 from anterior end, between right ocular peduncle and pneumostome. Bursa copulatrix duct varying from long to short, sometimes with a diverticulum. Vagina sometimes enclosed in a circum-vaginal gland. Epiphallus simple, lacking a flagellum, or absent. Phallus with or without an appendix, sometimes armed internally with spines. Central nervous system with long cerebropedal connectives, the right one slightly shor-ter than the left. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral ganglion chain moder-ately concentrated.

Haploid chromosome number 26.

Remarks. The Cochlicopidae comprise the four genera *Cochlicopa* d'Audebard de Férussac, 1821, *Azeca* Fleming, 1828, *Hypnophila* Bourguignat, 1858, and *Cryptazeca* de Folin & Bérillon, 1877.

Genus *Cochlicopa* d'Audebard de Férussac

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)
Turbo of authors. (Not *Turbo* of Linnaeus, 1758, type species *Turbo petholatus* Linnaeus, 1758, designated by de Monfort (1810); Turbinidae.)
Bulimus of authors. (Not *Bulimus* of Scopoli, 1786–88, type species *Bulimus haemastomus* Linnaeus, 1758, designated by Gray (1847) – synonym of *Megalobulimus* Miller, 1878; Acavidae.)
Oleacina of authors. (Not *Oleacina* of Röding, 1798, type species *Oleacina volutata* Röding, 1798 = *Bulla voluta* Gmelin, 1791, by monotypy; Oleacinidae.)

Achatina of authors. (Not *Achatina* of de Monet de Lamarck, 1799, type species *Bulla achatina* Linnaeus, 1758, by monotypy; Achatinidae.)
Columna of authors. (Not *Columna* of Perry, 1811, type species *Buccinum columna* Müller, 1774, by monotypy; Achatinidae.)
Glandina of authors. (Not *Glandina* of Schumacher, 1817, type species *Glandina olivacea* Schumacher, 1817 = *Oleacina voluta* Gmelin, 1791, by monotypy – synonym of *Oleacina* Röding, 1798; Oleacinidae.)
Cochlicopa d'Audebard de Férussac, 1821: 54 (as sub-genus of *Helix* Müller, 1774), type species *Helix lubrica* Müller, 1774, designated by Gittenberger (1983).
Ferussacia of authors. (Not *Ferussacia* of Risso, 1826, type species *Ferussacia gronoviana* Risso, 1826, according to Pilsbry (1908 (1908–10)); Ferussaciidae.)
Achatinella of authors. (Not *Achatinella* of Swainson, 1828, type species *Monodonta seminigra* de Monet de Lamarck, 1822 = *Turbo apexfulva* Dixon, 1788, designated by Pilsbry & Cooke (1912–14); Achatinellidae.)
Cionella Jeffreys, 1830: 347, type species *Helix lubrica* Müller, 1774, designated by Kobelt (1880 (1876–81)).
Zua Leach, in Turton, 1831: 82, type species *Helix lubrica* Müller, 1774, by monotypy.
Styloides Fitzinger, 1833: 105 (in part), type species not designated. For *Buccinum acicula* Müller, 1774, in Ferus-saciidae, and *Helix lubrica* Müller, 1774, in Cochlicopidae.
Folliculus de Charpentier, 1837: 14, type species *Helix lubrica* Müller, 1774, by monotypy.
Hydates Parreyss, 1849: 98, type species *Helix lubrica* Müller, 1774, by monotypy.
Opeas of authors. (Not *Opeas* of Albers, 1850, type species *Stenogyra goodalli* Miller, 1822 = *Bulimus pumilus* Pfeiffer, 1840, designated by von Martens (1860); Subulinidae.)

Diagnosis. Shell less than 8 mm in height; aperture lacking barriers, but thickened within by a callous rim continuous to upper insertion. Prostatic gland large, extensively fused to female pallial gonoduct to form a sperm-oviduct. Bursa copulatrix duct rather long, with a short diverticulum. Epiphallus well developed. Phallus with appendix well developed, lumen lacking spines.

Remarks. *Cochlicopa* d'Audebard de Férussac, 1821 and *Cionella* Jeffreys, 1830 are strict synonyms in having the same type species, *Helix lubrica* Müller, 1774. Most European malacologists at present accept *Cochlicopa* as the valid name, as was done also until relatively recently by American workers, including Pilsbry (1908 (1908–10)) in his earlier revision of the genus. Pilsbry later (1948 (1939–48)) decided that *Cionella* was the correct name, being influenced by Kennard's (1942) claim that d'Audebard de Férussac's *Cochlicopa* was an invalid name. Watson (1943) has shown, however, that Kennard's interpretation of the rules of nomenclature was erroneous in this instance. The same conclusion was reached by

Gittenberger (1983). Both *Cochlicopa* and *Cionella* are in current use by American malacologists. I concur with Bequaert & Miller (1973), following Watson in accepting *Cochlicopa* and Cochlicopidae as the oldest available generic and family names for *C. lubrica*.

Five species belonging to *Cochlicopa* have been described from Europe: *C. lubrica* (Müller, 1774), *C. lubricella* (Porro, 1837), *C. repentina* Hudec 1960, *C. nitens* (Gallenstein, 1848), and *C. pseudonitens* Uvalieva, 1967. *C. lubricella* was long considered to be a variety of *C. lubrica* (Germain 1930, Mermod 1930, Adam 1947) until Quick (1954) redescribed it as a species in its own right. Hudec (1960) later established further differences between the two species, and introduced *C. repentina* as a new species with characteristics intermediate between those of *C. lubrica* and *C. lubricella*. Most European authors currently consider *lubrica* and *lubricella* to be distinct species, but Adam (1960), Waldén (1965), Paul (1975), Kerney & Cameron (1979), Gittenberger (1983), and others find difficulty in distinguishing between the two taxa. *C. lubrica* and *C. repentina* are regarded as conchologically indistinguishable (Hudec 1960, Falkner 1992, Armbruster 1995).

A recent study of genital and conchological variability in *Cochlicopa* from Spain by Outeiro *et al.* (1990) has further questioned the validity of the specific status of *C. lubricella* and *C. repentina* as distinct from *C. lubrica*. Canonical discriminant analyses on shell characters by Armbruster (1995) indicate that both *C. lubricella* and *C. nitens* are conchologically distinguishable from *C. lubrica*. The studies of genital characters by Armbruster (1994) strongly suggest, however, that *C. lubrica* and *C. repentina* are merely seasonal or ecological variants of a single species. On the basis of shell morphometrics in *Cochlicopa*, Starobogatov (1996) recognised 27 species belonging to two subgenera in Eurasia, including all five European species listed above. Further study of the European *Cochlicopa* is needed, especially anatomically, to fully resolve the true limits of *C. lubrica*. For this reason I have refrained from including *C. lubricella* and *C. repentina* as junior synonyms of *C. lubrica*. The record of *C. lubricella* from Avondale, Auckland by Whitten (1957) is here referred to *C. lubrica*.

North American *Cochlicopa* were lumped under *C. lubrica* by Pilsbry (1948 (1939–48)) and Bequaert & Miller (1973). However, the genus is represented there by several species (Hubricht 1985).

Cochlicopa lubrica (Müller)

Figures 34, 74, 115, 144, 170, 196, 224, C8, M3, M4, M51–53, M113; Map 7

lubrica Müller, 1774: 104 (*Helix*).
muscorum Pennant, 1777: 131 (not of Linnaeus, 1758) (*Turbo*).
glaber da Costa, 1778: 87 (*Turbo*).
subcylindrica Gmelin, 1791: 3652 (not of Linnaeus, 1758) (*Helix*).
? *splendidula* Gmelin, 1791: 3655 (*Helix*).
stagnorum Pulteney, 1799: 49 (*Helix*).
exigua Menke, 1830: 29 (*Achatina*) (nude name).
minima von Siemaschko, 1847: 111 (*Achatina*).
buddii Dupuy, 1849: 330 (*Zua*).
lubricoides Stimpson, 1851: 54 (*Bulimus*).
?*azorica* Albers, 1852: 125 (*Glandina*).
maderensis Morelet, 1873: 242 (not of Lowe, 1852) (*Glandina*).
?*columna* Clessin, 1875: 41 (as variety of *lubrica* Müller, 1774) (*Cionella*).
?*crassula* Fagot, 1879: 23 (*Zua*).
locardi Pollonera, 1885: 695 (*Zua*).
lata Ping, 1929: 23 (*Opeas*).

Shell (Fig. 34, M3, M4) elongate oval, to 7.8 mm high by 2.5 mm wide; spire gradually widening from an obtuse apex, of 5.5–6 moderately convex whorls, thin, smooth, yellowish corneous, subtransparent and very glossy, imperforate; protoconch of approximately 1.5 whorls, smooth; aperture subvertical, ovate, without barriers, the outer lip evenly arcuate, bordered with yellow or red outside, in mature snails having a narrow, smooth, and continuous callous rib within; columella somewhat straightened, calloused, often very indistinctly notched or sinuous at its junction with basal lip; parietal callus thin, transparent.

Animal with sides of foot, mantle collar, and sole pale to dark grey; mantle collar speckled white, with flask-shaped glands. Foot rather short in active animal; sole indistinctly tripartite.

Reproductive system, Fig. 74. Ovotestis comprising 4 lobes, each made up of numerous acini, embedded in upper lobes of digestive gland. Hermaphrodite duct moderately long, distended and convoluted in its middle section, terminating in carrefour region with a small, bulbous talon partially embedded in albumen gland. Female pallial gonoduct sacculate, in its middle section differentiated by a zone of morphologically distinct glandular cells. Free oviduct rather short, stout. Vagina long. Bursa copulatrix duct rather stout at its origin on oviduct, but for the greater part rather slender, ending in a saccular reservoir, and giving off a short diverticulum at about same level as origin of vas deferens. Prostatic gland rather long, fused to female pallial gonoduct section to form spermoviduct; follicles most strongly developed in proximal part

but weak or absent in middle section, adjacent to specialised middle section of female tract. Vas deferens slender, accompanying free oviduct and then folding back around right ocular retractor to run to epiphallus, into which it abruptly expands. Epiphallus generally arched, opening into phallus with a small vergic papilla immediately distad of phallus retractor muscle insertion. Phallus rather slender, internally with fleshy stimulatory pads in proximal section, bearing apically an appendix with a bulbous base giving rise to a glandular sac on a slender duct. Atrium short, somewhat indistinct.

Spermatophore unknown.

Phallus retractor muscle arising from anterior part of diaphragm, to insert on distal epiphallus without branching.

Jaw (Fig. 115) aulacognathic, 0.5 mm wide, composed of about 20 narrow plates denticulating the lower border.

Radular ribbon (Fig. M51–53) with about 80 transverse rows of teeth, each with the formula 12–15+7–9+C+7–9+12–15. Central tooth narrow, tricuspid, with prominent mesocone and poorly developed but distinct ectocones, on an elongate basal plate. Lateral teeth somewhat larger than central tooth, bicuspid, with large mesocone and well developed ectocone, on a rectangular basal plate. Marginal teeth multicuspid, with mesocone first rounded then becoming serrate, and ectocone also becoming progressively more serrate towards margin of ribbon.

Digestive tract, Fig. 144. Buccal mass spheroidal. Oesophagus long, terminating in gastric pouch without a crop. Gastric pouch cylindrical, extending about half a whorl to end in a sacculate stomach which is not externally differentiated. Intestine producing a short, anteriorly directed loop to abut the kidney, then describing a posteriorly directed loop before again turning forwards and running to anus in mantle collar.

Pallial complex, Fig. 170. Pulmonary cavity in active animal extending for about 1 whorl. Kidney proper short, barely exceeding length of pericardium, extended to about 0.8 of pulmonary cavity length by a slender ureteric pouch. Retrograde closed ureter absent, but a ciliated groove extending for a short distance from excretory orifice towards top of pulmonary cavity. Pulmonary vein with no large branches.

Free muscle system, Fig. 196. Columellar muscle dividing below origin into left and right bundles. Left bundle giving rise first to buccal retractor, then dividing into ocular and inferior tentacular retractors. Right columellar branch giving rise near its base to a broad tail fan, divided more anteriorly into ocular and inferior tentacular retractors. Inferior retractor on both sides sending out a branch which ramifies to anterior cephalic body wall.

Central nervous system, Fig. 224. Cerebral commissure length about equal to cerebral ganglion width. Cerebropedal connectives subequal in length, the right one about equal to cerebral ganglion width. Pleural ganglia slightly closer to cerebral ganglia than to pedal ganglia. Parietal ganglia closer to visceral ganglion than to pleural ganglia; right parietal ganglion fused with visceral ganglion, which lies to right of median plane.

Haploid chromosome number 26.

Type material. Müller (1774) did not give a type locality with his species description. His material is assumed to have come from Frederiksdal near Copenhagen, Denmark. The whereabouts of this material is unknown; it is probably lost.

Distribution. Holarctic and circumpolar in natural range. Widespread in Eurasia, from Iceland, northern Europe, and Siberia south to northwestern Africa and east to Japan; in North America from north of the Arctic Circle in Alaska, south to Alabama in the east and at high elevations to Mexico. Introduced into St Helena, South Africa, Venezuela, Australia, and New Zealand.

Recommended common name. Slippery moss snail.

Material examined. New Zealand. Kermadec Is. Raoul I., Mt Campbell, Dec 1997, T. McGluggago. Raoul I., Expedition Hill, Dec 1997, T. McGluggago. Raoul I., Fishing Rock, Dec 1997, T. McGluggago. **ND.** Cape Maria van Diemen, Motuopao I., 27 Sep 1988, R. Parrish (MONZ M89818). Houhora, at motor camp, 1 Jan 1976, B.F. Hazelwood, (MONZ M70097). Mangapa Valley, Oct 1984, P.C. Mayhill (MONZ M83063). Herekino Gorge, 4 Jan 1976, B.F. Hazelwood (MONZ M48693). Herekino State Forest, Oct 1978, P.C. Mayhill (MONZ M62528). Mangamuka, Mangataipo Scenic Reserve, 2 Jun 1987, R. Parrish (MONZ M99168). Waima, Jan 1990, P.C. Mayhill. Whangarei, Mair Park, undated, R.K. Dell (MONZ M5385); Sep 1978, P.C. Mayhill (MONZ M83085). Kamo, R. Parrish, 17 Jul 1993. Whangarei Heads, Taurikura Bay, May 1961, W. Ponder (MONZ M20428). Waipu Caves, 9 Sep 1984, B.F. Hazelwood (MONZ M80228). Dargaville, Montgomery's Bush, Apr 1983, P.C. Mayhill (MONZ M82715). **AK.** Te Hana, 23 Feb 1994, in pasture. Hoteo, 20 Apr 1987, B.F. Hazelwood & H. Taylor. Omaha Forest, Aug 1987, P.C. Mayhill. Warkworth, Thompson's Bush, 28 Sep 1983, B.F. Hazelwood (MONZ M75725). Warkworth, Kowhai Park, Oct 1981, P.C. Mayhill (MONZ M78675). Warkworth, 2 Mar 1985, B.F. Hazelwood (MONZ M75720). Mahurangi Regional Park, 31 Jan 1987, B.F. Hazelwood. South Kaipara Heads, 1987, R.N. Wrenn. Muriwai Beach Park, Jan 1981, P. Sudlow (MONZ M70793). Albany, M. Holloway & A.G. Stevenson (MONZ M84646). Hobsonville, RNZAF, Walker's Bush Track, Dec 1980, P. Sudlow (MONZ M70751). Henderson, 15 Oct 1978, B.F. Hazelwood (MONZ M63434, M63460); 26 Sep 1983, B.F. Hazelwood (MONZ M75571). Takapuna, R.K. Dell (MONZ M5384), M. Holloway

& A.G. Stevenson (MONZ M84647). Cockle Bay, 17 Jan 1988, B.F. Hazelwood. Orakei, Little Rangitoto Reserve, 6 Sep 1987, B.F. Hazelwood. Auckland Domain, Aug 1986, J.F. Goulstone. Panmure, 12 Dec 1987, B.F. Hazelwood. Mt Eden, undated, coll.? (MONZ M84645). Mt Eden, 19 Mar 1987, B.F. Hazelwood, scoria crater. Mt Eden, Cornwall Park, Jul 1987, J.F. Goulstone, in rock wall. Mt Albert, 20 Aug 1987, B.F. Hazelwood. Titirangi, 26 Sep 1983, B.F. Hazelwood (MONZ M78889). Mt Wellington, 14 Mar 1987, B.F. Hazelwood, scoria crater (MONZ M99540); 6 May 1987, B.F. Hazelwood, in gardens. Howick, 2 Aug 1987, J.F. Goulstone, in remnant forest. Orakei, Kepa Reserve, Aug 1985, J.F. Goulstone, in litter of remnant forest. Ellerslie, 4 Apr 1987, 20 Oct 1987, and 20 Dec 1987, B.F. Hazelwood. Mangere, Oct 1983, J.F. Goulstone (MONZ M78916). Manurewa, Idesia Place Reserve, Nov 1987, J.F. Goulstone, from litter in modified kahikatea/totara forest. Manukau, Murphy's Bush, Nov 1985, J.F. Goulstone, in remnant kahikatea forest. Papatoetoe, Puhinui, 1961 and 1962, W. Ponder (MONZ M16937, M20429). Kawakawa Bay, Jun 1987, J.F. Goulstone, in open coastal forest. Ponga, 13 Jun 1987, J.F. Goulstone, in forest litter. Hunua Ranges, Hunua Falls Track, Mar 1983, J.F. Goulstone, in forest litter. Clevedon, Oct 1984, J.F. Goulstone, in scrubland litter. Red Hills, Puke Kiwiriki Pa, 7 Sep 1986, J.F. Goulstone, in remnant forest. Paerata, Coulthards Scenic Reserve, Oct 1985, J.F. Goulstone, in remnant forest. Raventhorp, 13 Jul 1988, J.F. Goulstone, in remnant forest. Bombay, Mt William Reserve, May 1984, J.F. Goulstone, in forest litter. Waiuku, Jones Bush, 11–12 Feb 1981, F.M. Climo & D.J. Roscoe (MONZ M78554). **CL**. Whitianga, 29 Apr 1992, D. Edinges. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. Thames, 15 Dec 1979, in grassy coastal bank. **WO**. Port Waikato, 1970–72, S. Easterbrook-Smith (MONZ M45888). Huriwai River Track, Jan 1982, P.C. Mayhill. Turua, 16 Dec 1979, in garden. Limestone Downs, 13 Feb 1981, F.M. Climo & D.J. Roscoe (MONZ M77922). Waikaretu, Mannerings Bush, 17 Sep 1977, B.F. Hazelwood (MONZ M57336, M58267). Waikaretu, Dec 1977, P.C. Mayhill. Te Aroha, 5 Nov 1977, B.F. Hazelwood (MONZ M57542). Hamilton, 15 Oct 1977, B.F. Hazelwood (MONZ M68530); 7 Jan 1977 and 20 Mar 1979, in gardens. Te Akau, Sep 1981, P.C. Mayhill. Tauwhare, 4 Feb 1995, in pasture. Maungakawa, Aug 1979, P.C. Mayhill. Maungakawa, Aug 1985, P.C. Mayhill. Raglan, Waimai Valley, 1970–72, S. Easterbrook-Smith (MONZ M39056); 1 Dec 1977, B.F. Hazelwood (MONZ M68552). Whatawhata, 21 Dec 1993, in limestone outcrops in remnant *Beilschmiedia tawa* forest. Ohaupo, 12 May 1980, concrete walls; 15 Mar 1993 and 8 Mar 1994, in garden. Waitomo, 2 Jul 1978, B.F. Hazelwood (MONZ M63409); 19 Sep 1978 and 8 Dec 1978, limestone outcrops in pasture and remnant *Beilschmiedia tawa* forest. Piripiri, Moa Bone Cave, 1970–72, S. Easterbrook-Smith (MONZ M45652). Te Anga, Mangapohue Natural Bridge Reserve, Apr 1960, coll.? (MONZ M84644); 16 Oct 1977, B.F. Hazelwood (MONZ M57452). Te Anga, 11 Sep 1984, B.F. Hazelwood (MONZ M76421). Marokopa River, undated, W. Ponder (MONZ M20430). Piopio, Megs Graveyard Cave, 1982, P.R. Millener (MONZ M77407). Mahoenui Valley, 6–7 Mar 1977, F.M. Climo (MONZ M55984, M56212). Mahoenui Valley, Totoro Rd Cave, 5 Mar 1977, F.M. Climo (MONZ M56822). **BP**. Kaimai Range, Te Tuhi Track, Nov 1982, P.C. Mayhill. Otumoetai, 26 Dec 1988, B.F. Hazelwood. Tauranga, 1984, B. McFadgen, archaeological survey (MONZ M85973); 7 Oct 1991, V. Johnson. Mt Maunganui, 12 Sep 1986, in sand dunes. Papamoa Beach, Sep 1989 and Jun 1991, in sand dunes. Edgecumbe, 12 Jan 1996, P.J. Addison, in pasture. Whakatane, Hikutaia Domain, Oct 1977, J.F. Goulstone. Whakamarama, 3 Mar 1979, in grassy roadside. Raukokore, 15 Sep 1992, in disturbed coastal *Beilschmiedia tawaroa-Vitex lucens* forest. Whangaparaoa, 14 Sep 1992, under timber of ruined buildings. Waimana, 18 Sep 1979, in disturbed *Beilschmiedia tawa* forest. Waioeka, Urutawa State Forest, Jun 1987, P.C. Mayhill (MONZ M99253). **GB**. Wainui Beach, Jan 1976, G.A. Foreman. Waikaremoana, 22 Apr 1995, S.S. Jones. Gisborne, H.M. Evans (MONZ M9938). **TK**. Mokau River mouth, 5 Mar 1977, F.M. Climo (MONZ M56730). S Mokau River, 5 Mar 1977, F.M. Climo (MONZ M56739). Tongaporutu River mouth, 8 Mar 1977, F.M. Climo (MONZ M56578). New Plymouth, Jun 1954, Dept Agric. (MONZ). New Plymouth, Fitzroy, Oct 1956, D. Fisher (MONZ M10416). Te Wera State Forest, 15 Feb 1978, M. Stoodley, in poplar plantation. **HB**. Tangoio, 25 Feb 1988, D.J. Roscoe (MONZ M89491). Hastings, 23 Jul 1989, T.T. Albert. **WI**. Matemateonga, Wanganui R., 23 Oct 1987, V. Vercoe (MONZ M89848). Kai Iwi, 14 May 1977, B.F. Hazelwood (MONZ M56229). Wanganui, 13 Jun 1975, E.M. Andrews (MONZ M38709); E.Y. Wolf (MONZ M75356). Wanganui, St Johns Hill, 12 Sep 1989, C. Ogle (MONZ). **WN**. Levin, 3 May 1991, G.T. Brown. **NN**. Takaka, 4 Jun 1977, P.C. Mayhill. Motueka, 6 Oct 1994, in grassy area at rear of sand dunes. Aniseed Valley, 8 Mar 1986, C.C. Meikle.

Extralimital. England. Malham Cove, Yorkshire, 1970, coll. & det. R.A.D. Cameron. **Ireland**. Oughterard, Galway, 26 Aug 1990, in rock wall. **Scotland**. Auchincruive, Dumfries & Galloway, 12 Sep 1990, in garden. **Spain**. Santiago de Compostella, Galicia, Apr 1989, in gardens and grassy roadside areas. **U.S.A.** Lancaster, Pennsylvania, May 1994, in pasture.

History in New Zealand. *C. lubrica* was first recorded from New Zealand by Crosse (1893), without locality data. Suter (1913) and Thomson (1922) list only Auckland as a locality for this species. Whitten (1955) lists a number of Northland and Auckland localities, and New Plymouth, indicating that the species was widely distributed in the North Island by the 1950s. Barker (1982) stated that *C. lubrica* was "a long established and common snail, especially in the northern regions of the North Island... ." No South Island records for *C. lubrica* were available to Barker (1982).

During the present study *C. lubrica* was found to be widespread and common on Raoul Island in the Kermadec group, in the North Island, and in the Nelson region of the South Island.

Biology. In its native range *C. lubrica* is known from a wide variety of habitats, including grassland, arable land, woods, and gardens. Krull & Mapes (1952), who studied

C. lubrica on farmland in New York State, U.S.A., found the snails to be most abundant in wet places under bushes or shrubs, occurring in considerable abundance in grassy pasture and other dry habitats. In New Zealand this species is most prevalent in moist, shaded areas in gardens. It is often abundant in patches of remnant, modified forest, especially those in urban areas and on limestone rock outcrops. It is unknown from closed, relatively undisturbed native forest. During periods of dry weather the snails aestivate with the shell aperture sealed to the substrate by a thin, colourless epiphragm. During dry weather the animals may burrow into the soil.

Little is known of the biology of *C. lubrica* in New Zealand. As noted in the Northern Hemisphere (e.g., Mapes & Krull 1952, Quick 1954, Baker 1969), eggs and juveniles can be found at most times of the year but with a trend for greater abundance in winter and summer. No information is available on the abundance of individuals in New Zealand habitats, but estimates for grassland in Europe and North America range up to 577 snails per m^2 (Mapes & Krull 1952, Boyd 1960, Baker 1969). In a Polish *Alnus* forest Umiński & Focht (1979) recorded populations up to 60 per m^2. Their sampling indicated that *C. lubrica* took 21–24 months to reach maturity and that the adult snails lived in excess of one year. These observations concur with those of Krull & Mapes (1952) for populations in New York farmland.

Both in New Zealand and in their native range these snails are often found congregated in large numbers on rocks, stone walls, and concrete paths. The suggestion by Pilsbry (1948 (1939–48)) that these aggregations are associated with breeding has not been confirmed. *C. lubrica* is a species of deterministic shell growth: snails held in the laboratory commenced oviposition within 5 days of thickening of the peristome. The eggs are spherical to oval, with a greater diameter of 1.1–1.5 mm, and comprise a flexible shell (Fig. M113) of calcareous granules embedded in a gelatinous matrix. The eggs are deposited singly, and are frequently covered with strands of faecal material and plant litter. While rather variable in size, the male genitalia of all New Zealand *C. lubrica* dissected (*n* = 18) were always well developed. Outeiro *et al.* (1990) record but do not discuss the occurrence of aphallic specimens in their Spanish collections.

Armbruster & Schlegel (1994) presented allozyme data indicating the frequent occurrence of self-fertilisation in *C. lubrica*.

Mapes & Krull (1951) noted that *C. lubrica* fed upon both green and dead plant material under laboratory conditions, but found no evidence of green plants being consumed under natural conditions. In the present study, snails collected from coastal forest at Opoutere had tissues

from both live and dead leaves in their intestinal tracts.

Remarks. An introduction into the very extensive literature on *C. lubrica* is provided by Germain (1930), Pilsbry (1948 (1939–48)), Likharev & Rammel'meier (1952), Quick (1954), Bequaert & Miller (1973), Backhuys (1975), Schileyko (1984), Grossu (1987), Outeiro *et al.* (1990), and Starobogatov (1996).

Family EUCONULIDAE

Diagnosis. Herbivorous aulacopod snails, ovoviviparous or oviparous. Shell minute to small, with 5th whorl diameter less than 10 mm, capable of fully housing the retracted animal, or reduced and not able to accommodate the animal. Shell lappets often developed on mantle collar. Foot with a well developed suprapedal groove and foot fringe. Sole tripartite. Caudal mucus pit often overhung by a caudal horn. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw oxygnathic. Marginal teeth elongate, multicuspid or bicuspid but lacking endocones, on slender basal plates. Intestine with a single forward-directed loop. Kidney with a closed sigmoid ureter, opening at pneumostome. Right ocular retractor passing over phallus. Phallus retractor arising from diaphragm, inserted on epiphallus or phallus. Genital orifice located immediately behind right ocular peduncle or a little posteriad. Sometimes with a diverticular sac on the talon. Male and female pallial gonoducts fused to spermoviduct. Free oviduct often glandular. Bursa copulatrix weakly developed, opening to phallus, atrium, or vagina, or absent. Epiphallus often with a short flagellum. Phallus variably developed, often with a sheath; appendix often present.Central nervous system with short cerebropedal connectives, the left one often shorter than the right. Right pleural ganglion near right cerebral ganglion. Visceral ganglion chain moderately concentrated.

Haploid chromosome number 28.

Remarks. Baker (1928, 1941) treated these snails as a subfamily (Euconulinae) of the Helicarionidae, as did Solem (1966). I follow Tillier (1989) in giving the euconuloid snails family status.

The Euconulidae, comprising about 20 genera, are represented in most regions of the world, with maximum diversity in the central and west Pacific. The limits of many genera are uncertain, as the anatomy of many species has not been examined. The family is represented in New Zealand by a single naturalised species.

Genus *Coneuplecta* Möllendorff

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montford (1810); Helicidae.)

Zonites of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix algira* Linnaeus, 1758, by original designation; Zonitidae.)

Nanina of authors. (Not *Nanina* of Gray, 1834, type species *Helix citrina* Linnaeus, 1758, designated by Gray (1847) – synonym of *Naninia* Sowerby, 1842, in Ariophantidae.)

Naninia of authors. (Not *Naninia* of Sowerby, 1842, in error for *Nanina* Gray, 1843; Ariophantidae.)

Hyalinia of authors. (Not *Hyalinia* of Albers, 1850, type species *Helix cellaria* Müller, 1774, designated by von Martens (1860) – synonym of *Oxychilus* Fitzinger, 1833, in Zonitidae.)

Sitala of authors. (Not *Sitala* of Adams, 1865, type species *Helix infula* Benson, 1848, designated by Adams (1865); Ariophantidae.)

Trochonanina of authors. (Not *Trochonanina* of Mousson, 1869, type species *Helix mozambicensis* Pfeiffer, 1855, designated by Nevill, 1878; Ariophantidae. Not of Garrett, 1884, type species *Nanina schmeltziana* Mousson, 1865, by original designation – synonym of *Diastole* Gude, 1913, in Microcystinidae.)

Coneuplecta von Möllendorff, 1893: 64, type species *Helix scalarina* Pfeiffer, 1851, by original designation.

Durgellina Thiele, 1928: 135, type species *Durgellina vitrina* Thiele, 1928 = *Helix calculosa* Gould, 1852, by original designation.

Conibycus Thiele, 1928: 136, type species *Conibycus dahli* Thiele, 1928, by original designation.

Parasitala Thiele, 1929–31: 398, type species *Parasitala osuiniensis* Thiele, 1931, by original designation.

Sitalina Thiele, 1929–31: 635, type species *Conulus circumcinctus* Reinhardt, 1883, by monotypy.

?*Turrisitala* Iredale, 1933: 55, type species *Turrisitala normalis* Iredale, 1933, by original designation.

Oviparous species. Shell small, moderately conical, angulate, narrowly perforate, corneous to greenish-brown or reddish-brown, finely striated or costulate; aperture without armature; peristome thin, not continuous. Shell lobes absent. Radula with a 5-cuspid central tooth, and with no more than 2 lateral teeth which are almost as elongate as marginals and have more than one ectocone. Genital orifice immediately posterior to right ocular peduncle. Diverticular sac on talon. Free oviduct with a glandular zone. Bursa copulatrix present. Phallus without an appendix. Phallus retractor inserted on epiphallus. Cerebropedal connectives short, the left one shorter than the right. Pleural ganglia closer to cerebral ganglia than to pedal ganglia. Right parietal ganglion fused with visceral ganglion, which is on right of median plane.

Chromosome number not known.

Remarks. Snails of Asia, Indonesia, Philippines, New Guinea, northern Australia, and numerous islands in the Pacific. In the absence of a revision of the Indo-Pacific Euconulidae I have essentially followed the taxonomy established by Baker (1941), who regarded *Durgellina* Thiele, 1928, *Conibycus* Thiele, 1928, *Parasitala* Thiele, 1931, and *Sitalina* Thiele, 1931 as junior synonyms of *Coneuplecta* von Möllendorff, 1893 and yet applied *Durgellina* and *Sitalina* at subgeneric rank without providing subgeneric diagnoses. *Coneuplecta calculosa* (Gould, 1852) was assigned to the subgenus *Durgellina* as it is conspecific with the type species *D. vitrina* Thiele, 1928. Other authors, such as Zilch (1959–60), treat *Durgellina*, *Conibycus*, *Parasitala*, and *Sitalina* as genera distinct from *Coneuplecta*. The status of *Turrisitala* Iredale, 1933, tentatively placed in synonymy with *Coneuplecta* by Baker (1941), has not been resolved (Smith 1992).

The anatomy of most *Coneuplecta* species is not known.

Coneuplecta calculosa (Gould)

Figures 35, 75, 116, 145, 171, 197, 225, M5–8, M9–12, M54, M55, M114, M115; Map 8

calculosa Gould, 1852: 48 (*Helix*).
microconus of authors (not of Mousson, 1865).
pinnocki Liardeti, 1876: 100 (*Helix*).
vitrina Thiele, 1928: 136 (*Durgellina*).

Shell (Fig. 35) conoid-turbinate, convex basally, up to 5.5 mm high by 5 mm in diameter, narrowly perforate, distinctly angulate when young, becoming almost evenly rounded at 5 whorls, but always with a low peripheral tread, when mature with 5–6 rapidly increasing whorls, very thin, corneous to very pallid, horn-coloured at apex, dullish, with satin-like finish above but more glossy below. Protoconch (Fig. M5–8) of 1.5–2 whorls, with closely spaced, rounded growth-threads, beaded by subequally spaced, spiral, impressed lines. Teleoconch (Fig. M9–12) with growth threads and more widely spaced spiral striae separating broader wrinkles; growth threads obsolescent shortly below periphery; sutures deep. Umbilicus superficial, its width 0.06 of shell diameter. Aperture broad, evenly rounded; peristome thin; columella sharply and broadly reflected above, closing more than half the perforation.

Animal very pale, with brown coloration of viscera visible through foot tissues and shell. Tail elongate, extending well beyond shell in active animal; a poorly developed horn over caudal mucus pit. Sole tripartite. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Reproductive system, Fig. 75. Ovotestis consisting of 2 clusters each of 4 or 5 claviform lobes, embedded on dorsocolumellar side of digestive gland. Hermaphrodite duct rather short, for the greater part dilated but narrowing to its entry in talon, bearing a diverticulum. Spermoviduct short; prostatic gland with follicles confined to distal part. Free oviduct moderately long, with a glandular zone in medial part. Bursa copulatrix reservoir an oval sac on a short, stout duct; fine muscle threads arising from spermoviduct inserted on apex of reservoir. Vagina short. Vas deferens long. Epiphallus short, its entry to phallus apparently without a papilla. Phallus elongate, with proximal 0.75 thick-walled, closely packed internally with papillae; distal 0.25 thin-walled, its internal lining smooth or weakly ridged. Sheath heavy and muscular, surrounding greater part of proximal phallus, with bands to epiphallus and onto phallus retractor. Atrium short.

Phallus retractor arising from diaphragm, investing base of epiphallus. Vagina receiving a branch from right lateral retractor.

Jaw (Fig. 116) broadly crescentric, 0.45 mm wide, with a weak medial projection.

Radula (Fig. M54, 55) of about 135–155 V-shaped rows of teeth, each with the formula 130–135+1+C+1+130–135. Central tooth very elongate, with 5 cusps constituting the elongate mesocone, shorter but prominent ectocones, and very small secondary ectocones. Lateral teeth elongate, with prominent endocone, mesocone and ectocone, and with 2 small secondary ectocones. Marginal teeth multicuspid, with prominent mesocone and ectocone and several smaller secondary ectocones. All teeth on elongate basal plates.

Digestive tract, Fig. 145. Buccal mass spheroidal. Oesophagus long, without a crop. Gastric crop cylindrical. Stomach a simple curvature bearing ducts to digestive gland, not differentiated externally from gastric crop. Intestine short.

Pallial complex, Fig. 171. Pulmonary cavity 2.5× as long as it is wide, extending over about 0.7 whorls. Venation apparently absent apart from pulmonary vein. Kidney triangular, occupying about 0.25 of length of pulmonary cavity. Ureter sigmoid, running along anterior face of kidney to top of pulmonary cavity, then recurving to run adjacent to rectum, close to pneumostome.

Free muscle system, Fig. 197. Columellar muscle giving off buccal retractor muscle almost immediately and right and left tentacular retractors very shortly afterwards. Tentacle retractors arising dorsally from lateral retractors, each dividing anteriorly to insert on ocular peduncle and interior tentacle; right ocular retractor crossing over phallus.

Central nervous system, Fig. 225. Cerebral ganglia united by a very short commissure. Cerebropedal connectives short, the left one shorter than the right. Pleural ganglia nearer to cerebral ganglia than to pedal ganglia. Left parietal ganglia adjacent to left pleural ganglion. Right parietal ganglion fused with visceral ganglion, which is on right of median plane.

Type material. Described from Tahiti, Society Islands. Syntypes USNM 5465 (but see Baker 1941 for discussion on their status).

Distribution. Widely distributed on islands of the Pacific.

Recommended common name. Calculus cone snail.

Material examined. New Zealand. CL. Opoutere, Nov 1995, P.C. Mayhill, coastal forest, 140 m alt.; 29 May 1996, G.M. Barker & M.P. Barker, coastal forest, 15 m alt.

History in New Zealand. This is the first record of *C. calculosa* established in New Zealand, confirmed by collection of live material from the field.

Biology. *C. calculosa* is widely distributed in the Pacific, at altitudes from sea level to nearly 700 m, suggesting that it has a requirement for subtropical to tropical climatic conditions. It has evidently been carried from island to island by human agency (Baker 1941, Solem 1959). The Pacific collection records quoted by Baker (1941) suggest that it is arboreal. The species of Java are known to be arboreal on low vegetation (van Benthem Jutting 1950). In contrast, Smith (1992) states that it occurs in litter of closed forest in coastal Northern Territory, Australia. The New Zealand material was gathered from the soil surface under broadleaf forest litter. Only two live animals were found amongst several hundred shells collected, possibly indicating that those on the forest floor had fallen from vegetation above. Searches of vegetation to 2 m height did not, however, yield any specimens.

Oviparous. The eggs are spherical, about 0.85 mm in diameter, with a white shell (Fig. M114, 115) composed of calcite crystals.

Family FERUSSACIIDAE

Diagnosis. Herbivorous aulacopod snails, oviparous or ovoviviparous. Shell small, oblong or lanceolate, smooth and glossy, unicolorous, with apex blunt, aperture pyriform, and columella often bearing a prominent spiral fold and parietal wall a medial lamella, capable of housing retracted animal. Eyes unpigmented in *Cecilioides*. Foot with a well developed suprapedal groove and foot fringe. Suprapedal gland embedded in foot tissues. Caudal mucus pit present in some species. Buccal mass spheroidal or weakly oval. Jaw aulacognathic. Radula with marginal teeth short, on broad basal plates. Intestine with a single loop directed forwards. Kidney short, transversely extended to hindgut, which it may follow some distance forwards; ureter closed, retrograde, extending to anterior margin of pulmonary cavity, opening via separate ducts to rectum and to exterior near pneumostome. Anal gland present in pallial cavity above pneumostome. Buccal retractors arising from left branch of columellar muscle. Right ocular peduncle retractor passing forwards over phallus. Genital orifice a short distance posterior to right ocular peduncle. Male and female pallial gonoducts, below carrefour, separate or fused. Phallus retractor arising from diaphragm or from right branch of columellar muscle, inserted on apex of epiphallus and, in some genera, on phallic appendix. Bursa copulatrix duct rarely long, often dilated at entry to oviduct, where a pilaster may occur. Epiphallus compact, bulbous, applied intimately to proximal phallus, with a low vergic papilla, this often somewhat vestigial. Phallus with dilated proximal section occupied by pilasters and often a sacrobelum-like papilla, and bearing a variously developed lateral appendix; distal section tubular and somewhat slender. Central nervous system with cerebropedal connectives in length equal to or less than cerebral ganglion width; left and right connectives of similar length. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain moderately compact; right parietal ganglion fused with visceral ganglion.

Haploid chromosome number 30.

Remarks. Most systematists of the Stylommatophora have recognised the ferussaciids at the family level, with close affinities to the Achatinidae and Subulinidae. Pilsbry (1946 (1939–48)) regarded these snails as a subfamily of the Subulinidae.

The Ferussaciidae comprise 12 genera, mainly Eurasian. Their systematics has not been fully resolved, as the majority of species have not been studied anatomically.

In contrast to Watson (1928) and Giusti (1973, 1976), I take the bulbous structure at the proximal end of the male genitalia in Ferussaciidae to be the epiphallus rather than part of the phallus.

Genus *Cecilioides* d'Audebard de Férussac

Buccinum of authors. (Not *Buccinum* of Linnaeus, 1758, type species *Buccinum undatum* Linnaeus, 1758, designated by de Montfort (1810); Buccinidae.)

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Bulimus of authors. (Not *Bulimus* of Scopoli, 1786–88, type species *Bulimus haemastomus* Linnaeus, 1758, designated by Gray (1847) – synonym of *Megalobulimus* Miller, 1878; Acavidae.)

Achatina of authors. (Not *Achatina* of de Monet de Lamarck, 1799, type species *Bulla achatina* Linnaeus, 1758, by monotypy; Achatinidae.)

Polyphemus of authors. (Not *Polyphemus* of de Montfort, 1810, type species *Polyphemus volutata* Röding, 1798, by monotypy – synonym of *Oleacina* Röding, 1798; Oleacinidae.)

Columna of authors. (Not *Columna* of Perry, 1811, type species *Buccinum columna* Müller, 1774, by monotypy; Achatinidae.)

Cecilioides d'Audebard de Férussac, 1814: 48, type species *Bulimus acicula* Bruguière, 1789 = *Buccinum acicula* Müller, 1774, by monotypy – ICZN Opinion 335 (1955a: 48).

Cochlicopa of authors. (Not *Cochlicopa* of d'Audebard de Férussac, 1821, type species *Helix lubrica* Müller, 1774, designated by Gittenberger (1983); Cochlicopidae.)

Acicula Risso, 1826: 81, type species *Acicula eburnea* Risso, 1826 = *Buccinum acicula* Müller, 1774, by monotypy. (Not *Acicula* of Hartmann, 1821, type species *Bulimus lineatus* Draparnaud, 1801 [ICZN Opinion 344, 1955c: 313]; Aciculidae.)

Ferussacia of authors. (Not *Ferussacia* of Risso, 1826, type species *Ferussacia gronoviana* Risso, 1826, according to Zilch (1959–60); Ferussaciidae.)

Achatinella of authors. (Not *Achatinella* of Swainson, 1828, type species *Monodonta seminigra* de Monet de Lamarck, 1822 = *Turbo apexfulva* Dixon, 1788, designated by Pilsbry & Cooke (1912–14); Achatinellidae.)

Cionella of authors. (Not *Cionella* of Jeffreys, 1830, type species *Helix lubrica* Müller, 1774, designated by Kobelt (1880 (1876–81)); Cochlicopidae.)

Styloides Fitzinger, 1833: 105, type species *Buccinum acicula* Müller, 1774, designated by Pilsbry (1946 (1939–48)).

?*Belonis* Hartmann, 1840 (1840–44): 48, type species *Buccinum acicula* (author not given) = *Buccinum acicula* Müller, 1774, by monotypy.

Macrospira Swainson, 1840: 171, type species *Helix octona* Gmelin, 1789 = *Cecilioides acicula* (Müller, 1774), designated by Pilsbry (1931).

Caecilioides Herrmannsen, 1846: 150. Unnecessary amendment of *Cecilioides* d'Audebard de Férussac.

Stenogyra of authors. (Not *Stenogyra* of Shuttleworth, 1854, type species *Bulimus terebraster* de Monet de Lamarck, 1801, according to Zilch (1959–60); Subulinidae.)

Sira Schmidt, 1855: 5, listed in synonymy by Zilch (1959–60), type designation not traced.

Caecilianella Bourguignat, 1856b: 378, type species *Buccinum acicula* Müller, 1774, according to Pilsbry (1909 (1908–10)).

–58–

Glandina of authors. (Not *Glandina* of Schumacher, 1817, type species *Glandina olivacea* Schumacher, 1817 = *Oleacina voluta* Gmelin, 1791, by monotypy – synonym of *Oleacina* Röding, 1798; Oleacinidae.)

Aciculina Westerlund, 1886 (1886–87): 175 (as section of subgenus *Caecilianella* Bourguignat of genus *Cionella* Jeffreys), type species *Buccinum acicula* Müller, 1774, according to Pilsbry (1909 (1908–10)).

Diagnosis. Oviparous species. Shell very narrowly lanceolate, imperforate, transparent (weathering to opaque white); aperture pyriform, its height usually less than half that of shell, its outer lip arching forwards in middle, with columella concave and more or less distinctly truncate at base. Animal white or unpigmented, the eyes unpigmented. Sole undivided. Caudal mucus pit absent. Hermaphrodite duct terminating without a diverticular talon. Male and female pallial gonoducts fused to form a spermoviduct. Bursa copulatrix duct very short, without dilation at entry to oviduct. Epiphallus spheroidal, closely applied to phallus, which it enters via a small vergic papilla. Phallus with extensive proximal pilasters; lateral appendix, when pres-ent, poorly developed. Phallus retractor arising from dia-phragm, inserted apically on epiphallus.

Remarks. *Cecilioides* species are calcicolous, burrowing snails found deep in the soil or hidden under leaf litter. They occur naturally in western and southern Europe, southern Asia, and the tropics.

Several sections or subgenera of *Cecilioides* have been distinguished on the basis of shell characters (Pilsbry 1909–10 (1908–10), Thiele 1929–31, Zilch 1959–60).

Subgenus *Cecilioides*

Diagnosis. Shell with spire slender, columella distinctly truncate at base; columellar and parietal walls of aperture without a conspicuous callus, but a low parietal nodule sometimes developed.

Cecilioides (Cecilioides) acicula (Müller)

Figures 36, 76, 117, 146, 172, 198, 226, C9, M13, M14, M56, M57; Map 9

aciculum Müller, 1774: 150 (*Buccinum*).
octona Gmelin, 1791: 36 (in part) (*Helix*).
? *obtusulum* Jacob, 1798: 639 (*Buccinum*).
terrestre Montagu, 1803: 248 (*Buccinum*).
eburnea Risso, 1826: 81 (new name for *acicula* Müller, 1774) (*Acicula*).
aciculoides de Cristofori & Jan, 1832: 2 (*Columna*).
miliaris de Cristofori & Jan, 1832: 2 (*Columna*).

pusilla Scacchi, 1836: 16 (*Achatina*).
acuta Companyo, 1837: 92 (*Achatina*) (nude name).
alba Brown, 1837–49: 32 (*Achatina*) (nude name).
gundlachi Pfeiffer, 1850: 80 (*Achatina*).
spiculum Benson, 1856: 434 (*Achatina*).
? *veru* Benson, 1856: 435 (*Achatina*).
anglica Bourguignat, 1856b: 384 (*Caecilianella*).
liesvillei Bourguignat, 1856b: 385 (*Caecilianella*).
aglena Bourguignat, 1857: 15 (*Caecilianella*).
hyalina Bielz, 1860: 296 (*Acicula*).
enhalia Bourguignat, 1860: 158 (*Caecilianella*).
rizzeana Benoit, 1862: 245 (*Achatina*).
stephaniana Benoit, 1862: 246 (*Achatina*).
gemmellariana Benoit, 1862: 248 (*Achatina*).
uniplicata Bourguignat, 1864a: 55 (*Caecilianella*).
bugesi Bourguignat, 1866 (1863–70): 184 (*Ferussacia*).
lactea Moitessier, 1867: 371 (*Caecilianella*).
amoenitatum Dohrn, 1869: 10 (*Caecilianella*).
mauriana Bourguignat, 1870: 54 (*Caecilianella*).
merimeana Bourguignat, 1870: 54 (*Caecilianella*).
tiberiana Benoit, 1875: 136 (*Achatina*) (nude name); Benoit, 1882: 89 (*Caecilianella*).
eucharista Servain, 1880: 121 (*Caecilianella*).
riberoi Servain, 1880: 131 (*Caecilianella*).
?*cristallina* Benoit, 1882: 90 (*Caecilianella*).
lauta Paulucci, 1886: 46 (*Acicula*).
gattoi Westerlund, 1892 (1892–94): 195 (*Cionella (Caecilianella)*).
melitensis Westerlund, 1892 (1892–94): 196 (*Cionella (Caecilianella)*).
pollonerae Westerlund, 1892 (1892–94): 196 (*Cionella (Caecilianella)*).
?*innovata* de Gregorio, 1896: 206 (*Caecilianella*).
praeclara Westerlund, 1898: 176 (*Caecilianella (Acicula)*).
retteri von Rosen, 1903: 181 (*Caecilianella*).
danica Schlesch, 1906: 184 (as a var. of *octona* Gmelin) (*Stenogyra*).

Shell (Fig. 36) very narrowly lanceolate with regularly tapered spire, 4.5 mm high by 1.2 mm in diameter, with 5 or 6 scarcely convex whorls, polished and smooth except for very weak spiral striae, thin, transparent, tinged yellow or golden brown in live specimens owing to colour of underlying digestive gland, imperforate; protoconch (Fig. M13, M14) blunt, rounded, smooth or with faint growth lines; aperture pyriform, 0.3 of shell height, narrowed and acute above, rounded at base, with outer lip thin and flexuous, and parietal wall not calloused; columella slightly calloused, with a columellar fold in juveniles, and abruptly truncate at its union with basal margin of aperture lip in adults.

Animal white, with eyes unpigmented. Active animal with head and tail much elongated, the latter often lifted off substrate but not reaching behind shell.

Reproductive system, Fig. 76. Ovotestis occupying uppermost whorls of viscera, consisting of a single large,

unpigmented acinus. Hermaphrodite duct proximally straight and slender, but distally much dilated and convoluted, at entry to talon slender and bent back upon itself in a U-shape. Albumen gland large, linguiform. Male and female pallial gonoducts fused into spermoviduct condition; walls of female part dilated but not apparently folded; male part a narrow internal groove passing along entire ventral side, into which open follicles of prostatic gland. Free oviduct short. Bursa copulatrix a small oval sac on a short, slender duct. Vagina rather long. Vas deferens very slender, inserted apically on male genitalia, adjacent to retractor muscle attachment. Male genitalia an ovoid, bulbous structure on a slender stem to atrium; proximal third of bulb, delimited by a slight constriction, representing vestigial epiphallus, internally with much folded walls; entry into phallus with a small vergic papilla. Proximal region of phallus occupied for the most part by several large pilasters; distally lumen free immediately before narrowing to extend to short, slender atrium.

Spermatophore unknown, probably not produced.

Phallic retractor arising as a slender branch of right division of columellar retractor system.

Jaw (Fig. 117) 0.3 mm wide, crossed by 26–28 folds which denticulate the edges.

Radular ribbon (Fig. M56, 57) with about 80 transverse rows of teeth, each with the formula 10 + 5 + C + 5 + 10. Central tooth small and narrow, with a short mesocone flanked by minute ectocones. Lateral teeth larger, tricuspid, on quadrate basal plates. Marginal teeth rather broad, bearing 6 or 7 minute cusps.

Digestive tract, Fig. 146. Buccal mass spheroidal to weakly oval. Oesophagus slender and long, extending to gastric pouch without formation of an oesophageal crop. Gastric pouch capacious, extending 0.7 of a whorl, constricted before giving rise to stomach. Intestine issuing from upper reaches of stomach to extend directly fowards before describing a posteriorly directed loop of about half a whorl, then running forwards to anus. Anal gland associated with anus in pulmonary cavity.

Pallial complex, Fig. 172. Pulmonary cavity extending around entire body whorl in adult, shorter in juveniles. Kidney short, barely exceeding length of pericardium, but prolonged transversely across top of pulmonary cavity to abut hindgut. Ureter closed, extending across anterior margin of kidney and then along hindgut to mantle collar, there opening via minute ducts to rectum and to body exterior below pneumostome. Vascular network of pulmonary cavity roof and main pulmonary vein weakly developed.

Free muscle system, Fig. 198. Columellar muscle with a short common stem, dividing into left and right branches. Left branch giving rise to buccal retractor and, further forward, to tentacle retractors and anterior pedal retractor. Right branch quickly giving off a broad but rather short tail fan; main stem dividing further forward into tentacular retractors and anterior pedal retractor; right branch to ocular peduncle passing over phallus.

Central nervous system, Fig. 226. Cerebral commissure shorter than cerebral ganglion width, rather slender. Left and right cerebropedal connectives equal, their length about equal to width of cerebral ganglion. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Left parietal ganglion separated from both left pleural ganglion and visceral ganglion by short connectives, but closer to visceral ganglion. Right parietal ganglion separated from right pleural ganglion by a short connective but fused to visceral ganglion, the latter lying to right of median plane.

Haploid chromosome number unknown.

Type material. Müller's material was collected from Thuringia – Thangelstedt near Weimar, Germany. The whereabouts of this material is unknown, and it is presumed lost.

Distribution. The natural range of *C. acicula* is believed to be central and western Europe, the Mediterranean, Arabia, North Africa, and Central Asia. Introduced to Northern Europe, the U.S.A., Bermuda, Barbados, Hawaii, the Azores, the Canary Islands, South Africa, Australia, and New Zealand.

Recommended common name. Blind pin snail.

Material examined. New Zealand. AK. Epsom, La Roche (MONZ M84650). Tamaki, 1 Nov 1993, B.F. Hazelwood. **BP**. Tauranga, 1984, B. McFadgen (MONZ M86174).

Extralimital. England. East Moen, Hampshire, 1979, coll. & det. R.A.D. Cameron.

History in New Zealand. First reported from New Zealand by Suter (1913). Further material was collected from the Epsom, Mt Eden, and Mt Albert areas in Auckland City in the 1950s (Whitten 1955). An established population was discovered near Tauranga in 1984 during archeological excavations, and the species is known from Nelson (D. Roscoe, pers. comm.), indicating that it may be more widespread than is suggested by the material in malacological collections.

Biology. Largely subterranean in habit, and in Europe most frequently encountered in rather dry pastures and other grassy areas, gardens, and caves. Also well known from graves in Europe, where the snails can be found in numbers associated with bones (see Pilsbry 1909–10

(1908–10) for review).

Definitive information on the food of *C. acicula* is lacking, but these snails are believed to feed on vegetable matter such as fungi and possibly fine roots.

Wächtler (1929a, b) describes various aspects of the biology of *C. acicula*, which is oviparous. Eggs 0.75 mm in diameter, with a calcareous shell, are laid singly in the soil.

Remarks. An introduction to the very extensive literature on *C. acicula* is provided by Watson (1928, 1929), Wächtler (1929b), Germain (1930), Pilsbry (1946 (1939–48)), Likharev & Rammel'meier (1952), Backhuys (1975), Giusti (1973, 1976), and Martinez-Orti *et al.* (1990).

Family HELICIDAE

Diagnosis. Herbivorous snails with shell capable of housing animal. Sole undivided. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw odontognathic, with degree of plate fusion variable. Radula with marginal teeth broad, on short basal plates. Intestine with a single forward-directed loop. Kidney with a retrograde closed ureter opening between lung top and pneumostome, or at pneumostome. Cephalic retractors strongly developed, arising as a single stem from columella, with right ocular retractor passing forwards between phallus and vagina. Phallus retractor arising from diaphragm. Genital orifice immediately behind right ocular peduncle, or a short distance posteriad. Accessory organs of genitalia comprising a single stylophore and 2 tubular, often branched, mucus glands opening into vagina. Bursa copulatrix reservoir adjoining pericardium, on a long duct with a diverticular branch. Phallus with a vergic papilla, and sometimes with a pseudopapilla arising from phallus wall. Central nervous system with cerebropedal connectives in length less than or equal to twice cerebral ganglion width, the left connective often longer than the right one. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 22–30.

Remarks. The Helicidae are European and circum-Mediterranean. Nordsieck (1987) recognised them as comprising two groups, the Ariantinae and Helicinae. In Schileyko's (1991) system the genus *Euparypha* Hartmann, 1843 is separated out from the latter group to form the monogeneric subfamily Euparyphinae.

The escargots or edible snails of Europe belong to this family, and members of several genera have been widely introduced, often becoming pests in their new range.

Subfamily HELICINAE

Diagnosis. Shell moderate-sized to large, commonly turbinate or globose, more rarely flattened; aperture lacking parietal barriers, but prominences or plates often present on basal and palatal margins; columellar margin sometimes with a callus. Genitalia with mucus glands variously ramified, with a minimum of 2 branches. Bursa copulatrix duct with diverticulum variously developed, sometimes reduced or absent, never bound to spermoviduct by a vascular membrane. Central nervous system with cerebropedal connectives in length less than twice cerebral ganglion width, the left connective generally longer than the right one.

Haploid chromosome number 22–30.

Remarks. The subfamily comprises about 26 genera, one of which is represented in New Zealand by a single naturalised species.

Genus *Cantareus* Risso

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Serpula of authors. (Not *Serpula* of Linnaeus, 1758, type species *Serpula vermicularis* Linnaeus, 1767, designated by Hartman (1959); Annelida.)

Cornu von Born, 1778: 371, type species *Helix aspersa* Müller, 1774, by monotypy (introduced for a teratological specimen).

Cochlea of authors. (Not *Cochlea* of da Costa, 1778, type species *Helix pomatia* Linnaeus, 1758, designated by Winckworth (1926); Helicidae.)

Acavus of authors. (Not *Acavus* of de Montfort, 1810, type species *Helix haemastomus* Linnaeus, 1758, according to Gude (1914); Acavidae.)

Helicogena of authors. (Not *Helicogena* of d'Audebard de Férussac, 1821, type species *Helix melanostoma* Draparnaud, 1801, according to Pilsbry (1894 (1890–95)); Helicidae.)

Cantareus Risso, 1826: 64, type species *Helix naticoides* Draparnaud, 1801 = *Helix aperta* Born, 1778, by monotypy.

Pomatia of authors. (Not *Pomatia* of Leach, in Turton, 1831, type species *Pomatia antiquorum* Leach, 1819 = *Helix pomatia* Linnaeus, 1758, by monotypy – synonym of *Helix* Linnaeus, 1758; Helicidae.)

Cryptomphalus de Charpentier, 1837: 5, type species *Helix aspersa* Müller, 1774, designated by Moquin-Tandon (1855).

Coenatoria of authors. (Not *Coenatoria* of Held, 1838 (1837–38), for *baspersa, lucana, lutescens, pomatia,* etc., – synonym of *Helix* Linnaeus, 1758; Helicidae.)

Tapada Gray, 1840: 127, type species *Helix aperta* von Born, 1778, by monotypy.

Callunea of authors. (Not *Callunea* of Scudder, 1882: 56, type species *Helix pomatia* Linnaeus, 1758,according to Pilsbry (1939 (1939–48)) – synonym of *Helix* Linnaeus, 1758; Helicidae.)

Megastoma of authors. (Not *Megastoma* of Scudder, 1882, type species *Helix pomatia* Linnaeus, 1758, according to Pilsbry (1939 (1939–48)) – synonym of *Helix* Linnaeus, 1758; Helicidae.)

Erctella di Maria di Monterosato, 1894: 168, type species *Helix mazzullii* de Cristofori & Jan, 1832, by monotypy.

Diagnosis. Shell moderate-sized, globose, imperforate, with peristome either simple or expanded; protoconch smooth. Jaw with strong ribs denticulating both margins. Kidney triangular, rather longer than the pericardium on its left side, occupying 0.25–0.5 of lung length. Secondary ureter closed to pneumostome. Genital orifice a short distance posterior to right ocular peduncle. Bursa copulatrix on long duct, with well developed diverticulum. Epiphallus well developed, with a long flagellum. Two mucus glands on vagina, with long tubular branches. Dart sac large, containing a single dart with 4 blades and a fluted base. Phallus subdivided to proximal and distal portions by robust annular pad; proximal phallus with papilla and a pseudopapilla; distal phallus with small pleats and crest-like structure at entry to atrium. Phallus nerve from right cerebral ganglion.

Haploid chromosome number 27.

Cantareus aspersus (Müller)

Figures 37, 77, 100, 118, 147, 173, 199, 227, 248, C10, C11, M15, M58–60, M116; Map 10

aspersa Müller, 1774: 59 (*Helix*).
hortensis Pennant, 1777: 136 (not of Müller, 1774) (*Helix*).
vulgaris da Costa, 1778: 72 (*Cochlea*).
copiæ von Born, 1778: 371 (*Cornu*).
lucorum de Razoumowsky, 1789: 274 (not of Müller, 1774) (*Helix*).
grisea Gmelin, 1791: 3649 (in part) (not of Linnaeus, 1758) (*Helix*).
variegata Gmelin, 1791: 3650 (*Helix*).
cornucopiae Gmelin, 1791: 3745 (*Serpula*).
rufescens Costa, 1839: 19 (*Helix*).
secunda Costa, 1839: 19 (*Helix*).
conoidea Moquin-Tandon, 1855: 175 (as subsp. of *aspersa* Müller) (not *conoidea* Draparnaud, 1801) (*Helix*).
spumosa Lowe, 1861: 111 (*Helix*).
solidissima Paulucci, 1879: 119 (as subsp. of *aspersa* Müller) (*Helix*).

depressa Paulucci, 1879: 120 (as subsp. of *aspersa* Müller) (*Helix*). (Not *Helix depressa* of Montagu, 1801 = *Skenea planorbis* (Fabricius); Skeneidae).
minor Paulucci, 1879: 120 (as subsp. of *aspersa* Müller) (*Helix*).
putris di Maria di Monterosato, 1892: 25 (*Helix*).
eutecta di Maria di Monterosato, 1892: 26 (*Helix*).
insolida di Maria di Monterosato, 1892: 26 (*Helix*).
mazzulopsis Pilsbry, 1893 (1890–95): 238 (*Helix (Pomatia)*).
subaperta Ancey, 1893: 136 (*Helix*).
cirtensis Kobelt, 1903: 98 (as subsp. of *aspersa* Müller) (*Helix*).
betae Trechmann, 1938: 17 (*Helix (Cryptomphalus)*).

Shell (Fig. 37) globose, to 33 mm high by 38 mm in diameter, of 4.5 whorls, the last whorl descending in front, dull yellow with 4 or 5 broad dark brown bands, the bands often broken up into blotches. Postembryonic whorls covered with strong transverse striae and, on the later whorls, a network of coarse irregular wrinkles imparting a shagreened appearance. Protoconch (Fig. M15) of 1.5 whorls, smooth, uniformly pale fawn. Aperture obliquely oval to almost circular. Peristome white, glossy, not continuous, with lip slightly reflected but not thickened. Columella erect and reflected, usually closing umbilicus in adults.

Animal pale brown, greenish brown, or blackish-grey, dark on dorsal aspect of head and paling slightly to foot margin; mantle collar blackish-grey, closely and finely sprinkled with pale grey-yellow; tubercles on head prominent, with pale summits; sole pale grey. Tail extending well beyond shell in active animal. Locomotion by muscular pedal waves generated from posterior of sole.

Reproductive system, Fig. 77. Ovotestis with acini clustered as an elongate mass, embedded in posterior lobe of digestive gland. Hermaphrodite duct of moderate length, the first part slender and straight, the medial part distended and strongly convoluted, then narrowing in distal part to talon at base of the large linguiform albumen gland. Spermoviduct rather long and slender; female part much folded; prostatic part a ribbon of acini along entire length. Free oviduct rather short, slender. Bursa copulatrix duct long, broad at its origin in oviduct but soon becoming very slender, giving rise at about 0.28 of its length to a very long and slender diverticulum; bursa copulatrix reservoir a spheroidal to oval sac, bound to diaphragm in region of pericardium by fine connective tissue. Vagina short, its proximal part bearing a large bulbous stylophore with paired mucus glands; stylophore armed internally with a calcareous dart about 10 mm long, its flared coronate base embedded in apical stylophore wall, its 4-bladed shaft directed into vagina; mucus glands each arising from vagina as a short, stout stem before branching into 10–16 tubular, slender diverticula. Vas deferens very slender, inserted at apex of epiphallus,

adjacent to origin of very long, slender flagellum. Epiphallus sinuous, cylindrical, forming a broad arch or sharply folded into a U-shape, entering phallus with a small, spheroidal, finely nodulate papilla. Phallus rather short; proximal part bulbous, housing a solid pseudopapilla arising from walls, separated from distal part by a prominent annular pad; distal phallus bearing weak longitudinal folds or crests that fuse to a pilaster-shaped pleat on distal vaginal wall. Atrium very short.

Spermatophore (Fig. 100) with anterior section about 32 mm long and 1 mm wide, comprising 5 longitudinal ridges that spiral gradually throughout its length; ridges smooth. Mid-section or body spindle-shaped, about 13 mm long and about 3 mm in maximum diameter; 4 longitudinal ridges from anterior part extending over entire length of mid-section, their crest irregularly serrate. Tail a whip-like filament, 80 mm in length, for the greater part U-shaped in cross-section and lacking ornamentation.

Phallus retractor arising from diaphragm, inserted on epiphallus a little proximal to its insertion on phallus.

Jaw (Fig. 118) about 3.7 mm wide, broadly crescentic, with anterior cutting margin strongly concave, scored with a variable number of prominent vertical ribs or folds strongly denticulating the upper and lower margins, and with distinct transverse striation.

Radula (Fig. M58–60) with about 125 transverse rows of teeth, each varying around the formula 23+20+C+20+23. Central tooth tricuspid, on a quadrate basal plate, with a broadly elongate mesocone and short but distinctly pointed ectocones. Lateral teeth tricuspid or bicuspid, on a quadrate basal plate, with mesocone broader and shorter than on central tooth, endocone generally absent, and ectocone small but distinct; 20th tooth transitional, with mesocone bifurcated and ectocone more prominent. Marginal teeth on small, broadly rectangular basal plates, of 3 or 4 cusps owing to division of mesocone and ectocone; teeth on outermost parts of radular ribbon often represented by basal plates lacking cusps.

Digestive tract, Fig. 147. Buccal mass spheroidal. Oesophagus slender and short, abruptly giving rise to a dilated crop. Stomach separated from crop by a constriction, short but dilated, occupying about 0.5 of penultimate whorl. Intestine extending in a short anteriorly directed loop to abut kidney, then producing a short posteriorly directed loop before running forwards to anus in mantle collar.

Pallial complex, Fig. 173. Pulmonary cavity short, in active animal about 2× longer than wide, extending to about 0.5 of body whorl; venation of roof strongly developed. Kidney triangular, extending to about 0.3 of pulmonary cavity length, with pericardium extending along the greater part of its left wall. Ureter sigmoid, closed to pneumostome, rather broad in its primary arm

along anterior of kidney but rather slender in its secondary part along rectum.

Free muscle system, Fig. 199. Columellar muscle extending forwards as a broad tail fan, attaching to pedal and lateral body walls, and near its origin giving rise to paired tentacular retractors, each of which divides anteriorly into branches to ocular peduncle, inferior tentacle, and cephalic body wall. Right ocular retractor passing across phallus. Buccal retractor originating from columellar stem adjacent to and immediately in front of tentacular muscles, extending anteriorly as a broad ribbon, then bifurcating before its attachment to posterior and lateral aspects of buccal mass.

Central nervous system, Fig. 227. Cerebral commissure moderately short. Left cerebropedal connective slightly longer than the right, in length about 1.5× width of cerebral ganglion. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Right parietal ganglion fused to visceral ganglion and closely appressed to left pleural ganglion. Left parietal ganglion apparently partially fused to visceral ganglion and closely appressed to left pleural ganglion. Visceral ganglion to left of median plane.

Haploid chromosome number 27.

Type material. Described from material collected in Italy. The whereabouts of this material is unknown, and it is presumed lost.

Distribution. Native in Western Europe to the borders of the Mediterranean Sea and Black Sea. Introduced to parts of Europe and North Africa as far back as the eighth century B.C. with the Phoenician, Greek, and then Roman settlements and trading posts established around the Mediterranean. Subsequently introduced into further European countries, southern Russia, Israel, the Azores, Madeira, St Helena, the Canary Islands, Canada, the U.S.A., Mexico, Bermuda, Haiti, Guatemala, Dominican Republic, French Guiana, Ecuador, Peru, Chile, Argentina, Brazil, West Africa, Zimbabwe, South Africa, Réunion, Tristan d' Acunha, Ascension, Mauritius, the Mascarene Islands, Taiwan, New Caledonia, the Loyalty Islands, Pitcairn, Easter Island, Australia, and New Zealand. Introductions were often unintentional with garden plants and freight, but not infrequently deliberate as a food snail.

Recommended common name. Brown garden snail.

Material examined. New Zealand. ND. Motuopao I., 27 Sep 1988 and 20 Oct 1989, R. Parrish. Spirits Bay, Dec 1974, in dunes. Spirits Bay, 7 Mar 1985, C. Ogle (MONZ M77150). Hooper Point, Maungapiko Hill, 11 May 1991, J.F. Goulstone. Great Exhibition Bay, Rarawa Beach, 15 Sep 1971, F.M. Climo

(MONZ M25630). Houhora, 27 Aug 1979, R. Zondag. Doubtless Bay, Dec 1956, J.C. Yaldwyn, in sand dunes (MONZ M12089). Kaitaia, 14 Sep 1971, F.M. Climo (MONZ M25604). Rawhiti Bay, 19 Sep 1971, F.M. Climo (MONZ M25622). Maunganui Bluff, Jan 1991, in gardens and coastal cliffs. Matapouri, 28 Sep 1971, A.N. Baker (MONZ M26033). Peach I., Whangarei, 13 Jun 1956, D. Garner (MONZ). **AK.** Te Hana, 11 Oct 1993, in grassy area at roadside. Goat I. Bay, Leigh, 5 Dec 1979, B.F. Hazelwood, under *Phormium* on coastal cliffs. Warkworth, Jul 1988, B.F. Hazelwood. Wenderholm beach, 29 Dec 1986, B.F. Hazelwood & H. Taylor. Tiritiri I., 23 Nov 1961, A. Wright (MONZ M14119). Beehive I., 1 Mar 1989, A. Tennyson (MONZ M99622). Onehunga, 23 Sep 1978, B.F. Hazelwood, under hedge. Blockhouse Bay, 4 Oct 1986, B.F. Hazelwood & H. Taylor. Mt Eden, 3 March 1987, B.F. Hazelwood. Ellerslie, 12 Jul 1987, B.F. Hazelwood (MONZ M99492). Hunua Ranges, Cossey's Dam Track, Aug 1979, J.F. Goulstone. N Waiuku Beach, 14 Jan 1978, B.F. Hazelwood (MONZ M69264). **CL.** Whitianga, 29 Apr 1992, D. Edinges. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. Karangahake Gorge, 31 Aug 1988, D.J. Roscoe (MONZ M92684). **WO.** Te Akau, Sep 1981, P.C. Mayhill. Whatawhata, 21 Dec 1993 and 3 Jan 1994, in limestone outcrops in pasture and remnant *Beilschmiedia tawa* forest. Karamu, 27 Jan 1996, in broadleaf scrub and pasture. Eureka, 15 Jan 1995, in gardens. Cambridge, Maungakawa Reserve, 1977, P.C. Mayhill (MONZ M57541). Matangi, 18 Jul 1980, R.N. Watson, in commercial asparagus. Ohaupo, 8 Nov 1992, 15 Mar 1993 and 8 Mar 1994, in gardens. Te Mata, Bridal Veil Falls Scenic Reserve, 27 Jan 1996, in broadleaf scrub and pasture. Oparau, 15 Aug 1977, B.F. Hazelwood (MONZ M62583). Mangapohue, 16 Oct 1977, B.F. Hazelwood (MONZ M57384). Waitomo, 18 Feb 1981, F.M. Climo (MONZ M77476). **BP.** Waihi Beach, 20 Jan 1994, in sand dunes. Mt Maunganui, 12 Sep 1986, in sand dunes and gardens. Papamoa, 3 Jan 1995, in dunes. Matata, 12 Sep 1986, in sand dunes. Opotiki, 12 Sep 1986, in sand dunes. Raukokore, 15 Sep 1992, in disturbed coastal *Beilschmiedia tawaroa-Vitex lucens* forest. Whangaparaoa, 14 Sep 1992, under *Lupinus arboreus* and *Muehlenbeckia complexa* in dunes. Mamaku, 25 Jan 1996, in *Leptospermum* scrub. Tawera, nr Whakatane River, May 1977, J.F. Goulstone. **TO.** Aratiatia, 25 Jan 1996, in broadleaf scrub. Tongariro National Park, nr Rangipo, 1 Feb 1996, in *Leptospermum* scrub. **GB.** Te Araroa, 21 Sep 1992, under *Muehlenbeckia complexa* and drift logs on gravel dunes. Rangiata, 20 Sep 1992, in disturbed coastal *Vitex lucens-Beilschmiedia tawaroa-Dysoxylum spectabile* forest. Gisborne, 22 Sep 1991, G. Foreman. Hopuruahine Landing, Lake Waikare-moana, May 1978, J.F. Goulstone, rock rubble in *Melicytus* scrub. Wairoa, 22 Sep 1991, G. Foreman. Mahia Peninsula, 20 Sep 1991, G. Foreman. **RI.** Ngamatapouri, 2 Apr 1972, D.J. Roscoe (MONZ M96839). **TK.** New Plymouth, 8 Sep 1993, in gardens. Oakura, 9 Sep 1993, in grassy area of coastal cliff. Okato, 4 Oct 1988, snail farm. **HB.** Waimarama, 8 Mar 1977, B.F. Hazelwood (MONZ M55722, M70704). Waipukurau, 8 Mar 1977, B.F. Hazelwood (MONZ M55776). **WI.** Waitotara, 3 Apr 1972, D.J. Roscoe (MONZ M98112). Ashhurst, 27 Nov 1976, B.F. Hazelwood (MONZ M55284). Santoft State Forest, Turakina, 1977, I.R. Millar, associated with *Lupinus arboreus*

under *Pinus radiata* on coastal dunes. **WA.** Castlepoint, 1 Feb 1963, R.K. Dell, in sand dunes (MONZ M16498); Apr 1991, P.C. Mayhill. **WN.** Makairo, 3 Jan 1982, B.F. Hazelwood (MONZ M75760). Otaki, Waltons Bush, 11 Dec 1983, B.F. Hazelwood (MONZ M79757). Waikanae, 1957, W. Ponder (MONZ M18627). Paekakariki, McKays Crossing, 23 Feb 1980, B.F. Hazelwood (MONZ M63173). Porirua, 1957, A.G. Beu, in sandhills (MONZ M32018). Upper Hutt, 15 May 1991. Lower Hutt, 1957, W. Ponder (MONZ M18631). Wellington, undated, Mestayer (MONZ), 1 Jul 1949, R.A. Falla (MONZ). Wellington, Somes I., 19 Oct 1954, R.K. Dell (MONZ M22152). Wellington, Ohiro Bay, 1975, N.J. Peterson (MONZ M57650). Wellington, Ngaio Gorge Track, 28 Dec 1974, F.M. Climo (MONZ M69157). Castlepoint, 1935, C.M. Hestor (MONZ). Wainuiomata, J.C. Yaldwyn (MONZ). **SD.** Long Beach, D'Urville I., 13 Nov 1943, W.R.B. Oliver (MONZ M11916). Picton, Victoria Domain, 25 Jan 1987, F.M. Climo (MONZ M86334). **NN.** Takaka, 6 Jan 1977, B.F. Hazelwood (MONZ M56147). Takaka Hill, 4 Jun 1977, B.F. Hazelwood (MONZ M56104). Motueka, 6 Oct 1994, coastal dunes and gardens. Nelson, 6 Oct 1994, city park, in *Phormium*. Cable Bay, 6 Oct 1994, in gardens. **KA.** Kaikoura Peninsula, First Bay, 20 May 1972, R.E. Fordyce (MONZ M72634). **BR.** S Inangahua Junction, 10 Oct 1982, F.M. Climo (MONZ M72991). **NC.** Weka Pass, Waikari, 17 Dec 1987, D.J. Roscoe (MONZ M97475). **MC.** Christchurch, 21 Sep 1991, L. Ford, in garden. Christchurch, 3 Oct 1991, A. Mannering, in gardens. **DN.** Dunedin, Flagstaff Hill, 16 Feb 1994, at margin of *Pinus radiata* plantation. Portobello, 16 Feb 1994, on grassy bank at harbour edge. Mosgiel, 12 Dec 1981, T.G. Watson; 15 Feb 1994, in gardens. **Chatham Is.** Waitangi, Jan 1979, coastal dunes.

Extralimital. Australia. Camden, New South Wales, Oct 1993, in gardens. Sydney, New South Wales, Oct 1993, in gardens. **Ireland.** Glenarm, Antrim, Aug 1990, on coastal limestone cliffs. **Spain.** Muros, Galicia, 18 April 1989, on coastal cliffs. **U.S.A.** Riverside, California, June 1986, in citrus orchards.

History in New Zealand. *C. aspersus* is popularly believed to have been first introduced into New Zealand by the French in the 1860s. The earliest record in New Zealand's malacological literature appears to be that of Hutton (1883), who lists Auckland, Nelson, and Greymouth as localities. However, the species was well established by that time, particularly at the seaport towns (Musson 1891, Suter 1891). Further, the snails are known to have been abundant in some districts as early as the 1860s (Thomson 1922). Damage in gardens and crops was reported in the 1890s (e.g., Broun 1897).

The pattern of greater abundance of *H. aspersa* in the North Island than in the South Island was evident by the early twentieth century (Thomson 1922).

Biology. *C. aspersus* is among the most widespread and abundant of the naturalised land snails. While present in

both North and South Islands, it is more common in the north. Generally it is most abundant in coastal areas, and becomes scarcer with increasing altitude and/or distance from the coast; nonetheless, it is abundant in some inland North Island districts. It is absent from closed-canopy native forest, but may occur in disturbed native forest or scrub on the coast and inland on limestone outcrops.

C. aspersus is highly prized by Europeans as an edible snail. It continues to be collected in vast numbers in the Mediterrenean area for human consumption but, as wild stocks are declining, there is increasing emphasis on farming (heliciculture). Currently the centre of commercial production is France, but significant quantities are produced in other Mediterranean countries such as Italy, Spain, and Greece. *C. aspersus* is also farmed for both local consumption and export in other parts of the world, including New Zealand. Heliciculture methods vary from simple outdoor pens to a largely automated indoor battery pen system. Information on commercial culture of *C. aspersus* can be found in Avagnina (1983), Chevallier (1983, 1985), Daguzan (1983, 1989), Elmslie (1982, 1989), Runham (1989), de Grisse (1991), and Associazione Nazionale Elicicoltori (1986–90). A consequence of this interest in heliciculture, and the importance of the species as a pest in several crops, is that there is considerable information available on the biology *C. aspersus*.

As to food plants, *C. aspersus* is selective, but feeding does occur on a large variety of living and dead plant tissues. A fundamental prerequisite of intensive heliciculture is the availability of suitable feed stock. It has been demonstrated that snails will grow at an acceptable rate on dry feed diets with high ash and relatively low protein content, provided they have access to water (Daguzan 1981). Studies on the performance of *H. aspersa* fed on commercially available animal feedstuffs demonstrated their preference for diets based on vegetable rather than animal protein (Stephanou 1986c, Jess & Marks 1989). The selection of raw materials, particularly the cereal component, is also known to be an important factor in the palatability of snail diets (Bittante 1984). *C. aspersus* consumes significant quantities of soil as part of its normal diet. In heliciculture, the provision of a soil substrate has demonstrated significant beneficial effects on snail growth rates (Gomot *et al.* 1986, 1989a, Jess & Marks 1989, Albuquerque de Matos 1990).

C. aspersus, like other helicids, is an obligate outcrossing species (Frömming 1954, Albuquerque de Matos 1989) highly sensitive to degeneracy effects of inbreeding. As may occur when farms are established from limited founder stock, or in severely depleted natural populations, inbreeding manifests first in fecundity and fertility, then in size and survivorship, till finally, within three or four generations of sib matings, the lines become wholly infertile (Albuquerque de Matos & Serra 1984, 1988, Albuquerque de Matos 1989). Each mature snail will mate several times in a single season, with an interval between matings of as little as 3 days (Basinger 1931). Observations on courtship behaviour in *C. aspersus* have been published by Herzberg & Herzberg (1962), Giusti & Lepri (1980), and in detail by Chung (1987) and Adamo & Chase (1988). In the course of the present study, courtship behaviour was observed in snails brought to the laboratory during the spring and summer months.

Three phases of courtship (Fig. 248) have been described by Chung (1987) and Adamo & Chase (1988). An introductory phase consists of labial-head contact behaviour. Each snail probes the head and labial region of the other with its mouth and labial palps. With the head raised off the substrate and the tentacles fully extended, the snails move their jaw and radula actively, intermittently biting or nuzzling each other. The genital pore shows some swelling, or the terminal genitalia may be partially everted. The second phase comprises labial probing of the genital region and dart shooting behaviour. Labial probing occurs when a snail presses its mouth and labial palps on the genital pore, or on the skin next to the genital pore of the partner. This behaviour can occur with or without genital eversion in either snail, although full genital eversion usually begins at this time. When the behaviour occurs simultaneously and reciprocally in both snails, the everted genitalia will be appressed and apposed. A snail usually assumes a characteristic body posture and behaviour, whereby the sole is contracted and reduced in size but the anterior head-foot becomes swollen and distended, with ocular peduncles shortened but not invaginated. The snail pushes its swollen and very turgid everted genitalia against its partner. Dart shooting occurs when a snail rapidly everts the dart sac from the vaginal region of the already everted terminal genitalia. The dart, which is attached by its base to the base of the dart sac, is rapidly pushed out so as to (usually) pierce the flesh of the partner. The dart carries approximately 2 mg of white mucus secreted by the glands associated with the stylophore (Chung 1986a). The dart sac is then withdrawn. The dart is never propelled through the air, but is torn from the dart sac on becoming lodged in the partner's tissues. Occasionally the dart either does not hit the partner or does not lodge in the flesh, and is then withdrawn partially or entirely back into the dart sac. The erotic impulse includes full phallus eversion simultaneously with, or shortly after, shooting the dart.

Contrary to assertions by Chung (1986b), snails engaging in courtship behaviour for the first time usually possess a dart (Giusti & Lepri 1980). Snails that have gone

through dart shooting within the previous 5–7 days (in an earlier courtship), and have not yet regrown a fully formed dart, eliminate this behaviour from their courtship.

Once dart shooting behaviour has occurred, the dart is not used again. Dissections by Chung (1987) showed that darts which fail to lodge in the partner's tissues are discarded into the producer's bursa copulatrix diverticulum shortly before reception of a spermatophore from the partner during copulation. A new dart starts to grow within 6 hours of expulsion of a dart, and is fully grown within 5–8 days (Giusti & Lepri 1980, Tompa 1982, Chung 1987).

The third courtship phase consists of repeated phallus eversion and attempted copulation. Snails enter into this phase of mating only after dart shooting behaviour, and do not depend on receipt of a dart from the partner. In the normal development of this phase the snail, while oriented with its everted atrium pressed against the body of the partner, exhibits a momentary tensing of the body wall of the anterior headfoot. This is followed immediately by increased turgor of the everted atrium and then by phallus eversion. The everted phallus invaginates immediately if the snail does not achieve successful intromission. If intromission fails, the snail usually pauses before attempting copulation again. Normally the everted atria of the two snails are apposed when phallus eversion occurs. However, a snail can also evert its phallus when the everted atrium is pressed against any other part of its partner, indicating that tactile stimulation of the genitalia is necessary for triggering of the penial eversion behaviour.

Courting animals can make as many as 50 intromission attempts, or as few as one, before achieving copulation. Copulation does not occur unless intromission is simultaneous. In successful intromission the everted phallus is allowed to penetrate the vagina of the partner and to lodge in the vaginal canal. The snail attaining intromission takes on the mating posture, in which the head is lifted off the substrate, the tentacles are shortened and held vertically, and the snail remains immobilised until it deposits its spermatophore into the partner's bursa copulatrix diverticulum. Adamo & Chase (1988) observed that usually only the second or third simultaneous intromission leads to successful spermatophore transfer. Transfer of the spermatophore to the partner is not strictly simultaneous for both snails. Once a snail has tranferred its spermatophore it comes out of the mating posture, retracts its phallus, and waits for its partner to finish.

Digestion of the received spermatophore occurs in the bursa copulatrix diverticulum (Giusti & Lepri 1980, Adamo & Chase 1988).

Giusti & Lepri (1980), Chung (1987), and Adamo & Chase (1988) observed that the duration of courtship in C. aspersus varies considerably. The time from start of court-ship to dart shooting averages about 35 minutes, while dart shooting to copulation takes another 15–45 or, rarely, as much as 240 minutes. Copulation was observed to last from 4 to 12 hours. Spermatophore transfer takes an hour or more towards the end of intromission.

Herzberg & Herzberg (1962), Cowie (1980), Giusti & Lepri (1980), Chung (1987), and Pos (1994a, b) have noted precocious mating in young C. aspersus lacking a deflected lip on the shell. These snails produce fertile eggs. For a South Auckland population, Pos (1994a) noted that over 30% of snails mated and 23% laid eggs before cessation of shell growth.

The function of the dart and of dart-shooting behaviour in the courtship and reproductive physiology of C. aspersus and other land snails has long been debated. Nonetheless, the function remains unclear (see Tompa 1984, Chung 1986a, 1987, and Adamo & Chase 1988 for the most recent discussions).

While courtship behaviour varies little, the reproductive output of C. aspersus varies greatly between individuals and populations. Studies of natural populations (Millar 1978), experiments in the laboratory (Herzberg 1965, Dan & Bailey, 1982) and experience in heliciculture (Lucarz 1984, Daguzan 1985, 1989, Marciano 1986, Stephanou 1986a, b, Elmslie 1989) show that crowding effects at high population densities result in reduced growth rate, increased mortality, and reduced and more variable adult snail weight, all of which contribute to reduced fecundity. Albuquerque de Matos (1989, 1990) found high heritability values for adult size, but diet has an overriding effect on snail growth rates and size at maturity. The season of the year in which snails are reproductive in the wild varies between populations and even among individuals within a population; this variation is largely governed by environmental conditions, but there is apparently a genetic component (Albuquerque de Matos 1989, 1990, Elmslie 1989). It has been well established (Bailey 1981, Enée et al. 1982, Le Guhennec & Daguzan 1983, Laurent et al. 1984, Gomot & Gomot 1985, Aupinel & Daguzan 1989, Gomot et al. 1989b, Lazaridou-Dimitriadou & Bailey 1991) that long days stimulate whereas short days inhibit growth rates and egg laying. While the first oviposition of the season is indifferent to photoperiod, long days are needed in order to induce more egg-layings (Enée et al. 1982).

A period of hibernation (or artificially imposed quiescence) has been shown to increase the reproductive activity and fecundity of C. aspersus (Bonnefoy-Claudet & Deray 1984). Hibernation in C. aspersus is controlled primarily by photoperiod, although temperature may determine its duration (Bailey 1981, 1983, Aupinel 1987); this hibernation condition is more correctly termed

diapause. Reproduction becomes non-seasonal within several generations when the snails are maintained under optimum conditions (Albuquerque de Matos 1990); three or four generations can be produced each year.

Like most Mediterranean snails, *C. aspersus* can survive in a dormant aestivatory state for many months during dry weather. Under New Zealand conditions the majority of mature snails begin mating in spring (October/November) and oviposition continues throughout the late spring, summer and autumn provided that activity is not arrested by aestivation during dry weather (Pos 1990, 1994a, b, G.M. Barker, unpubl. data). Millar (1978) found that *C. aspersus* populations increased following seeding of lupin (*Lupinus arboreus*) into Manawatu coastal dunes. Under these conditions of actively expanding populations, snails reached maturity in about 12 months. High snail numbers were maintained for as little as 3 years, however, as lupin growth and survival was adversely affected. In declining populations, Millar found that the snails required 2–3 years to reach maturity.

Egg laying commences 3–6 days after first fertilisation, but can occur within hours of subsequent matings. Under unfavourable conditions, egg laying in fertilised snails may be delayed by a period of aestivation (Basinger 1931). *C. aspersus* deposit their eggs into pockets in moist soil. These pockets are usually excavated by the snails themselves through movement of the head and anterior foot, though occasionally natural cavities will be used (Basinger 1931, Herzberg & Herzberg 1962, Pos 1990). Not all nest excavations that are initiated will be successfully filled with eggs; many are apparently abandoned before one is finally considered suitable. After oviposition the nests are covered with soil and are abandoned. The number of eggs in each clutch varies from 10 to 176 (e.g., Basinger 1931, Ingram 1947, Herzberg & Herzberg 1962, Daguzan 1989, Pos 1990, 1994a, b) and deposition of a single clutch may take as long as 36 hours (Pos 1990). Under optimum conditions in indoor farms, individual snails can produce 2500 eggs in a year (Runham 1989).

The eggs are spherical to oval, varying in greater diameter from 3 to 4.9 mm. The egg shell (Fig. M116) is partly calcified, with discrete crystals of calcium carbonate dispersed in the inner of two flexible jelly matrix layers. During embryogenesis the snail embryo dissolves and absorbs calcium from the egg shell (Tompa 1984). Guéméné & Daguzan (1983) observed that eggs produced by different snails varied from translucent to opaque, according to the quantity of calcium carbonate crystals in the egg shell. They were able to demonstrate that embryo development and hatching success were higher in those with high calcium provisions. Reproductive snails have a high calcium requirement (Tompa 1984), and egg produc-

tion by snails exposed to calcium-poor soil was approximately doubled when $CaCO_3$ was supplied (Crowell 1973).

The incubation period of the eggs has been shown by Guéméné & Daguzan (1983) to vary according to the relative humidity of the incubation environment. In one experiment at 20°C, for example, they recorded that the incubation period increased from 13.8 ± 1.9 days to 40.0 ± 9.9 days as the relative humidity declined from 100% to 70%. Survivorship of the eggs similarly declined with decreasing humidity, from 91.5% to 14%. The young hatchling snails remain in the nest for 1–16 days (Basinger 1931, Ingram 1947, Herzberg & Herzberg 1962). During this time, egg cannibalism can occur (Elmslie 1988).

Field populations of *C. aspersus* tend towards an annual breeding cycle. In laboratory culture, the animals tend not to exhibit any seasonality of breeding.

C. aspersus is gregarious, and very high numbers of snails can occur in favourable habitats such as garden shrubbery, coastals dunes and cliffs, and scrub on limestone outcrops. The gregarious behaviour is particularly apparent over the winter months, when the diapausing snails aggregate in protected sites. During this diapause hibernation the shell aperture is sealed with an epiphragm or several epiphragms. In the Manawatu dunes Millar (1978) observed hibernation to begin in May and to reach a peak in July. The snails became active again in mid August. According to Taylor (1906–14 (1902–21)) the juvenile snails are less sensitive to the cold and thus less inclined to diapause. There are few reported estimates of population size, but from an average of 40 snails per lupin plant Brockie (1957) estimated 20 000 snails per hectare in the Paekakariki dunes north of Wellington.

The species has a very well developed homing instinct. Snails return regularly to the same retreat each morning after their nightly forays.

The pest status of *C. aspersus* in New Zealand is discussed by Cederman (1951).

Remarks. *Cantareus* Risso, 1826 (type species *Helix aperta* Born, 1778) has long been recognised as a genus distinct from *Helix* Linnaeus, 1758 (type species *Helix pomatia* Linnaeus, 1758). Giusti *et al.* (1995) have demonstrated that *Helix aspersa* Müller, 1774 has strong systematic affinities with *Cantareus aperta*, and accordingly transferred this species to the genus *Cantareus*. Unlike members of *Helix*, species of *Cantareus* possess a solid pseudopapilla arising from the wall of the proximal phallus and a crestlike structure in the distal phallus that extends to and fuses with a pilaster-shaped pleat in the vagina.

Cantareus takes precedence over two supraspecific taxa

founded on *Helix aspersa* Müller, 1774. *Cryptomphalus* Charpentier, 1837 is junior by date of description with respect to *Cantareus*, and *Cornu* Born, 1778 is unavailable because it was deliberately introduced for a teratological (scalariform) specimen, and as such is excluded in terms of Art. 1 (b) (2) of the International Code of Zoological Nomenclature (1985).

Numerous varieties of *C. aspersus*, founded on shell variation, are recorded in the literature. Shell polymorphism in size, shape, markings, and colour has been extensively studied, with recognition of several endemic forms in North Africa (Taylor 1906–14 (1902–21), Chevallier 1977). Recent work on the genetic variability of allozymic characters (Crook 1981, Bleakney *et al.* 1989, Madec 1989, 1991) and life-history traits (Madec & Daguzan 1993) has suggested that the more distinct morphs, *C. aspersus aspersus* and *C. aspersus maximus* Taylor, can be recognised as subspecies. Guiller *et al.* (1994) found that the morphological heterogenic Moroccan populations could not, however, be distinguished by allozymic variation, thus again calling into question the subgeneric status of *C. aspersus maximus*. They raise the possibility that *C. aspersus maximus* is a 'man-made' morph, associated with early selective breeding in cultivation, rather than a natural morphotype.

Material from New Zealand (Auckland, Hokitika) was included in the allozyme study of Bleakney *et al.* (1989).

One of the principal helicid snails used for human consumption in Europe, especially the Mediterranean region, *C. aspersus* has been cultivated since at least the time of the Romans.

An introduction to the extensive literature on *C. aspersus* is provided by Germain (1930), Likharev & Rammel'-meier (1952), Giusti (1973, 1976), Backhuys (1975), Chevallier (1977), Cesari (1978), Schileyko (1978a), Guiller *et al.* (1994), Madec & Guiller (1994), and Giusti *et al.* (1995).

Family HELICODISCIDAE

Diagnosis. Herbivorous snails. Shell under 5 mm in diameter, strongly depressed, with few whorls that do not increase rapidly in size, always capable of fully housing the retracted animal; sculpture of spiral periostracal ridges or fringes, reduced in some taxa; aperture frequently with barriers or nodules, sometimes deflected and/or thickened when adult. Foot with a well developed peripodial groove. Sole uniform, with no waves of progression. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw polyplacognathic. Radula with marginal teeth broad, on short basal plates, sometimes lacking cusps on outermost teeth. Intestine with a single loop directed forwards. Kidney often with a small rectal lobe reaching to and often partially overlying the rectum, and with a closed retrograde ureter opening next to rectum at posterior of pulmonary cavity. Cephalic retractors arising almost at same level as separate branches from columellar stem. Right ocular retractor crossing phallus. Phallus retractor arising from diaphragm. Genital orifice immediately posterior to right ocular peduncle. Prostatic gland and oviduct fused to form a spermoviduct. Talon very elongated, without a distinctly expanded head. Phallus with or without a verge and pilasters, with or without a lateral caecum. Epiphallus frequently with a separate retractor muscle.

Central nervous system and chromosome number unknown.

Remarks. The helicodiscid snails have been widely recognised as having close affinities to the arionacean endodontoids. Their family status has long been disputed, however, reflecting the unstable systematics of the endodontoids. The subfamily unit Helicodiscinae, in the Endodontidae, was credited to Pilsbry in a paper by Baker (1927). It was defined on the basis of kidney form, with *Helicodiscus* Morse, 1864, *Chanomphalus* Strebel & Pfeffer, 1880, and *Radiodiscus* Pilsbry & Ferriss, 1906 included. Thiele (1929–31) and Pilsbry (1948 (1939–48)) excluded *Radiodiscus* and defined the subfamily on the basis of the ovotestis, shell coiling, and radula. Solem (1957) included *Polygyriscus* Pilsbry, 1948 in the Helicodiscinae, while later (Solem 1975) *Chanomphalus* and *Radiodiscus* were assigned charopid affinities.

The helicodiscoid snails have subsequently been variously accorded subfamily rank in the Endodontidae, Charopidae, Punctidae, and Discidae, or recognised as a separate family, Helicodiscidae. The latter is accepted here. The above family diagnosis is largely taken from Solem (1975, 1984a), who considered the Helicodiscidae to contain only three genera: *Helicodiscus* Morse, 1864 and *Polygyriscus* Pilsbry, 1948 from North America, and

Stenopylis Fulton, 1914 from Indonesia, the Philippines, New Guinea, the Solomon Islands, and Australia.

Genus *Helicodiscus* Morse

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Zonites of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix algira* Linnaeus, 1758, by original designation; Zonitidae.)

Hyalinia of authors. (Not *Hyalinia* of Albers, 1850, type species *Helix cellaria* Müller, 1774, designated by von Martens (1860) – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Helicodiscus Morse, 1864: 25, type species *Helix lineata* Say, 1817 (not of Olivi, 1792) = *Helicodiscus parallelus* (Say, 1821), by monotypy.

Phrixgnathus of authors. (Not *Phrixgnathus* of Hutton, 1883, type species *Helix fatua* Hutton, 1880 (= *Phrixgnathus celia* Hutton, 1883), designated by Pilsbry (1892–93 (1890–95)); Punctidae.)

Hydrophrea Climo, 1974: 271, type species *Laoma (Phrixgnathus) academia* Climo, 1970, by original designation and monotypy. **New synonymy.**

Diagnosis. Ovoviviparous species. Shell aperture without a reflected lip but usually with pairs of tubercles deposited at intervals on parietal and/or palatal walls. Animal generally unpigmented except for orange coloration on mantle collar in some species. Ocular peduncles rather stout, without swollen apices, and without pigmented eyes (animal blind). Ovotestis very long, unbranched, subcylindrical, occupying about 1 whorl in upper digestive gland. Phallus with a small vergic papilla but lacking pilasters. Radula with 3 or 4 tricuspid lateral teeth in each half row.

Remarks. *Helicodiscus* is known from Jamaica, Cuba, northern Mexico, and the eastern and northwestern U.S.A., regarded by most authors as the extant range of the genus. The occurrence of *Helicodiscus* in Europe and the Madeiran Archipelago has generally been attributed to stocks of *H. singleyanus* (Pilsbry, 1890) introduced from North America. Most such occurrences have been noted in habitats associated with the activities of man, such as greenhouses and gardens. However, the probability of European *Helicodiscus* being a natural occurrence has been raised by other collections of *H. singleyanus* having been made in areas remote from human disturbance (e.g., Chatfield 1977, Schlickum 1979) and the discovery of a *Helicodiscus* species endemic to the Tuscan Archipelago (Giusti 1976). The occurrence of *H. singleyanus* as an apparent subfossil in European Pleistocene strata (e.g., Ložek 1964) needs to be verified by dating of the shell material, because the species is frequently recovered as a contaminant of soil from archaeological excavations (Chatfield 1977; and see Remarks under *H. singleyanus*).

Three subgenera have been recognised (Pilsbry 1948 (1939–48)): *Helicodiscus* s. str., *Hebetodiscus* Baker, 1929 and *Pseudiscus* Morrison, 1942. These subgenera are based entirely on shell characters and have not been critically examined from the perspective of anatomy, which for many *Helicodiscus* is unknown.

Subgenus *Hebetodiscus* Baker

Hebetodiscus Baker, 1929: 86, type species *Helicodiscus (Hebetodiscus) singleyanus inermis* Baker, 1929, by original designation.

Hydrophrea Climo, 1974: 271, type species *Laoma (Phrixgnathus) academia* Climo, 1974 = *Helicodiscus singleyanus* (Pilsbry 1890), by monotypy and original designation. **New synonymy.**

Diagnosis. Shell entirely smooth or with microscopic spiral threads; aperture lacking internal teeth in adults.

Remarks. Bequaert & Miller (1973) regard *Hebetodiscus* as sufficiently distinct from *Helicodiscus* to be accorded generic rank, but give no details to support their assertion.

Helicodiscus (Hebetodiscus) singleyanus (Pilsbry)

Figures 38, 78, 119, 148, 174, 200, M16, M61–63; Map 11

scintilla Lowe, 1852: 115 (*Helix*).

singleyanus Pilsbry, 1889: 197 (*Zonites*) (nude name). Pilsbry, 1890–91 (1890–95): 84 (*Zonites*).

inermis Baker, 1929: 86 (as subsp. of *singleyanus* Pilsbry) (*Helicodiscus*).

laeviuscula Sterki, 1892: 53 (*Hyalinia*).

texana Sterki, 1892: 54 (*Hyalinia*) (nude name).

intermedius Morrison, 1942: 378 (*Helicodiscus (Hebetodiscus)*).

academia Climo, 1970: 211 (*Laoma (Phrixgnathus)*). **New synonymy.**

Shell (Fig. 38) strongly depressed, to about 2.4 mm in diameter by 0.9 mm high, of 4–4.5 tightly coiled, rounded whorls with deep sutures, thin, translucent white to pale straw, somewhat glossy with weak growth lines. Protoconch (Fig. M16) of 1.5 whorls, generally smooth but occasionally with fine microscopic spiral threads. Umbilicus widely open, 0.28–0.33 of shell diameter. Aperture lunate, with no teeth at any stage of growth. Peristome simple.

Animal unpigmented, translucent white. In active animal tail short, not extending behind shell, which tends to be dragged. Genital orifice immediately posterior to right ocular peduncle.

Reproductive system, Fig. 78. Ovotestis undivided, elongate, subcylindrical, embedded in digestive gland. Hermaphrodite duct not convoluted, slender at extremities, medially distended. Talon markedly elongate, slender, weakly expanded at apex, exposed on ventral surface of large, linguiform albumen gland. Pallial gonoducts fused to form spermoviduct; prostatic gland a ribbon along entire, rather sacculate glandular oviduct. Free oviduct stout. Bursa copulatrix reservoir small, elongate, on a long, slender duct. Vagina short. Vas deferens slender throughout. Epiphallus elongate, convoluted in proximal part, somewhat dilated medially. Phallus short, slightly dilated proximally at entry of epiphallus as a rounded vergic papilla; pilasters lacking, but internal wall somewhat glandular, thrown into weak longitudinal folds. Atrium distinct but short and slender.

Spermatophores unknown.

Phallus retractor originating from diaphragm, attaching at juncture of epiphallus and phallus. Epiphallus also provided with a retractor muscle, from the right tentacular retractor, inserted on epiphallus proximal apex.

Jaw (Fig. 119) a broad arch, about 0.4 mm wide, composed of 15 fused, approximately oval plates.

Radular ribbon (Fig. M61–63) with about 85 transerve rows of teeth, varying little about the formula 4+4+C+4+4. Central tooth narrower and often slightly shorter than 1st lateral tooth, tricuspid, the cusps rather small, with mesocone longer than the flanking ectocones; basal plate narrowly rectangular. Lateral teeth tricuspid, with elongate mesocone and short endocone and ectocone, on broad, quadrate basal plates. Marginal teeth serrate, with progressively shorter mesocone and progressively more divided endocone and ectocone; basal plate broad, short.

Digestive tract, Fig. 148. Buccal mass spheroidal. Oesophagus long, terminating in a gastric pouch without apparent crop formation. Gastric pouch subcylindrical, extending about 0.3 of whorl to end in sacculate stomach, which is not externally differentiated. Intestine producing a long, anteriorly directed loop to abut the visceral-pallial wall, then reflected to a short, posteriorly directed loop before running forwards to anus in mantle collar.

Pallial complex, Fig. 174. Pulmonary cavity long, about 2.5× length of kidney. Principal pulmonary vein without evident tributaries. Kidney extending anteriad to about twice length of pericardium, laterally with a small lobe abutting or partially overlying rectum. Primary ureter large, dilated, looped between limbs of kidney. Secondary ureter running adjacent to rectum, closed to about opposite middle of kidney and then continued by an open groove to near pneumostome.

Free muscle system, Fig. 200. Columellar muscle slender, on reaching base of haemocoele widening considerably to give off at almost the same level right and left tentacular retractors, large but very short buccal retractor, and small tail retractor with radiating fibres. Ocular branch of right peduncle retractor passing over phallus.

Central nervous system not examined.

Haploid chromosome number not known.

Type material. From New Braunfels, Comal County, Texas (ANSP 160058).

Distribution. *H. singleyanus* is endemic to North America, occurring naturally from New Jersey south to Florida, and west to Arizona. It has been introduced to California, and apparently also to Europe and New Zealand, where it now occurs.

Recommended common name. Singley's subterranean discus snail.

Material examined. New Zealand. CL. Little Barrier I., Shag Track, Aug 1983, P.C. Mayhill (MONZ M79503). **BP.** Tauranga, 1984, B. McFadgen (MONZ M85046, M85818, M85822). Paengaroa, Dec 1983, B. McFadgen (MONZ M78975). **WO.** Hamilton, 15 Oct 1977, B.F. Hazelwood (MONZ M68529). Newstead, 27 Jan 1994, in pasture. Te Kuiti, Mangaokewa Scenic Reserve, undated, B.F. Hazelwood, limestone shingle slide (MONZ M68875). **TO.** Tokaanu, The Knob, 23 Dec 1977, B.F. Hazelwood (MONZ M70839). **TK.** New Plymouth, Papakura Park, 5 Feb 1984, B.F. Hazelwood (MONZ M79787). **NN.** Rabbit I., 9 Aug 1972, G. Kuschel (MONZ). Nelson, 22 May 1972, G. Kuschel, from D. Lauria's well (MONZ); 24 May 1972 and 23 Jan 1973, G. Kuschel, from Nelson City Council nursery well (MONZ). Waimea, 14 Apr 1972, G. Kuschel, from Eden's bore no. 1 (MONZ); 22 May 1972, G. Kuschel, from F. Harrison Young's well (MONZ). **MC.** Holotype *Laoma (Phrixgnathus) academia* Climo, coll. Botany Dept, Univ. Canterbury, Quaternary deposit (contaminant) 2 m below a layer of Waimakariri River alluvium, University of Canterbury Ilam site, Christchurch (MONZ M23252).

History in New Zealand. *H. singleyanus* was first recorded by Climo (1970, 1974) from subterranean water sources at Christchurch and Nelson in the South Island (see Remarks). It has since been found at a number of localities in the North Island. It is highly probable that *H. singleyanus* has been long established in New Zealand, and is now widely distributed.

Biology. *H. singleyanus* apparently lives a predominantly subterranean existence in soil, and hence material collected alive is rare in collections. The most common source of material is flood drift. The animal is colourless and blind,

and is known to be ovoviviparous (Pilsbry 1948 (1939–48)).

Remarks. *Helix scintilla* Lowe, 1852 has priority over *Zonites singleyanus* Pilsbry, 1890. It is in accordance with ICZN Article 23b to render *scintilla* obsolete in favour of the well established name *singleyanus* (Pilsbry), but a case to ICZN for this action has not been made.

When *Laoma (Phrixgnathus) academia* was described from New Zealand (Climo 1970) the type specimen was assumed to be an original component of a Quaternary deposit, 400–500 years old, found beneath about 2 m of Waimakariri River alluvium. In 1974 further specimens were collected in water pumped from wells and bores near Nelson, also in the South Island (Climo 1974). The site of the original specimen and the habitat of the subsequent Nelson material seemed to suggest a snail of phreatic (aquatic, subterranean) existence, and led Climo (1974) to introduce the name *Hydrophrea*. In that paper shells, terminal genitalia, the foot, buccal mass, and radular teeth were illustrated. The shells (Climo 1974, fig. 5A–F) are typically those of subadult *Helicodiscus singleyanus* (Pilsbry 1948 (1939–48), fig. 346).

Anatomical features of the single dissected specimen (radula – fig. 5I; reproductive terminalia – fig. 5G) illustrated by Climo (1974) also point to *Hydrophrea academia* being a synonym of *H. singleyanus*. The number of teeth were four fewer in a half radular row in the New Zealand specimen than in H.B. Baker's dissection of New Jersey (U.S.A.) material. Climo's illustration does not show as much cusp detail as Baker's (Pilsbry 1948 (1939–48), p. 635, fig. 345), but the salient features are the same in both. The male terminal genitalia of Climo's New Zealand specimen match Baker's description for *H. singleyanus* (Pilsbry 1948 (1939–48), p. 637). While helicodiscid snails typically have a long bursa copulatrix duct (Pilsbry 1948, Solem 1975, 1984a), such a structure was described as absent in *H. academia* (Climo 1974). This may have been an error in observation (F.M. Climo, pers. comm.). The unpigmented body and eyes further point to *H. academia* being conspecific with *H. singleyanus* (Pilsbry 1948 (1939–48), Climo 1974).

Subsequently further specimens of this helicodiscid have been collected from a number of localities in the North Island, including a series of live animals from Tauranga and Hamilton. The anatomy and radula of these specimens are consistent in character with both *Hydrophrea academia* (except for the presence of a long bursa copulatrix duct) and North American *H. singleyanus*. There is a remote possibility, however, that *Helicodiscus* is an indigenous element of the New Zealand fauna.

H. singleyanus has a burrowing habit, and in friable soils and gravels could easily get into groundwater systems, hence the retrieval of Climo's specimens from wells and bores.

Bequaert & Miller (1973) note that among North American material the subspecies *H. singleyanus inermis* Baker cannot consistently be distinguished, even by geography, from typical *H. singleyanus*. Pilsbry (1948 (1939–48)) earlier admitted that these two forms are "so similar that their separation is most difficult." Hubricht (1975) has maintained that *singleyanus* and *inermis* are specifically distinct, with the shell smaller and having shallower sutures in *H. inermis*, and suggested that the difference in shell sculpture by which these two forms were originally differentiated is a poor character. Waldén (1983) has also maintained that *singleyanus* and *inermis* are distinct species, but gives no supporting information. Until the intrageneric phylogeny of *Helicodiscus* has been resolved from anatomical characters, *inermis* is best regarded as conspecific with *singleyanus*.

An introduction into the literature on *H. singleyanus* is provided by Pilsbry (1948 (1939–48)), Kuiper (1956), Bequaert & Miller (1973), Riedel & Wiktor (1974), Chatfield (1977), Flasar (1977), Schlickum (1979), and Altonaga (1989b).

Family HYGROMIIDAE

Diagnosis. Herbivorous snails. Shell small to moderate in size, capable of fully housing the animal; aperture with lip frequently present, situated at some distance from aperture margin. Animal with sole holopod, undivided. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw odontognathic, with ribs varied in development. Radula with marginal teeth broad, on short basal plates. Intestine with a single loop directed forwards. Kidney with a closed retrograde ureter, opening between top of lung and pneumostome, or at pneumostome; some taxa with a long ureteric diverticulum extending along rectum below ureter opening. Cephalic retractors arising as a common stem on columella; right ocular retractor sometimes passing between phallus and vagina, sometimes free from genitalia. Phallus retractor arising from diaphragm. Genital orifice located immediately behind right ocular peduncle, or somewhat more posteriad. Genitalia primarily with stylophores (when present, and not extremely regressed or modified) forming a dart-sac complex consisting of 1 or 2 double units with a common base and distinct distal sacs lying side by side in the same plane. Darts (when present) short to long, straight or slightly curved. Digitiform mucus gland tufts variable in number, inserted on proximal vagina, more-or-less close to where dart sacs open into vagina. Reservoir of bursa copulatrix

adhering to spermoviduct, not connected with wall of pulmonary cavity, its duct of medium length to short and lacking a diverticulum. Male genital ducts with a spermatophore-producing epiphallus, with flagellum. Phallus generally with a vergic papilla. Central nervous system with cerebropedal connectives in length less than twice cerebral ganglion width; left connective often longer than the right one. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 21–27.

Remarks. The Hygromiidae are a group of helicoids of western Palaearctic distribution, recently separated from the Helicidae as a distinct family. Several Hygromiidae have been widely distributed through the activities of man. Two genera – *Candidula* Kobelt, 1871 and *Prietocella* Schileyko & Menkhorst, 1997 – are each represented in the New Zealand naturalised fauna by a single species.

The scope and subfamilial systematics of the Hygromiidae continues to change as new data on anatomy and hence phylogenetic relationships are made available. Suprageneric names and diagnoses are consequently not attempted here. In his classification of the hygromiids, Nordsieck (1993) places *Candidula* Kobelt, 1871 in the Hygromiinae *Helicella-Candidula* Group (= Helicellini von Ihering, 1909) (with genera *Xerotricha* di Maria di Monterosato, 1892 and *Helicella* d'Audebard de Férussac, 1821), and *Cochlicella* d'Audebard de Férussac, 1821 in the Monachinae Cochlicellini Schileyko, 1972 (with the genus *Monilearia* Mousson, 1872). Schileyko & Menkhorst (1997) maintain that a close phylogenetic relationship exists between *Monilearia* and *Cochlicella*, which they formalised by creating the family Cochlicellidae. These authors also erected the genus *Prietocella* Schileyko & Menkhorst, 1997 for *Helix barbara* Linnaeus, 1758, which had long been included in the genus *Cochlicella*.

The systematic status of the cochlicellid snails has long been controversial, and for the present I have retained their placement in the Hygromiidae. The genus *Prietocella* is, however, accepted as several reproductive characters of the sole species, *P. barbara* (Linnaeus, 1758), distinguish this taxon from *Cochlicella* and *Monilearia*. In particular, *Prietocella* lacks the calcareous envelope around the phallus papilla that occurs in *Cochlicella*.

Recent works such as those by Nordsieck (1986b, 1987, 1993), Manganelli & Giusti (1987), Hausdorf (1988, 1990a, b, c), Giusti & Manganelli (1987, 1989, 1990b), Schileyko (1972, 1978a, b, 1979, 1991), Aparicio *et al.* (1991), Giusti *et al.* (1992), Puente & Prieto (1992), Gittenberger (1993a, b), and Schileyko & Menkhorst (1997) will provide the reader with an introduction to the extensive literature and the complexities of hygromiid systematics.

Genus *Candidula* Kobelt

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Helicella of authors. (Not *Helicella* of d'Audebard de Férussac, 1821, type species *Helix ericetorum* Müller, 1774 = *Helicella itala* (Linnaeus, 1758), designated by Herrmannsen (1847) [ICZN Opinion 431,1956: 350]; Hygromiidae.)

Jacosta of authors. (Not *Jacosta* of Gray, 1821, type species *Helix (Jacosta) albella* Draparnaud, 1801 = *Helix explanata* Müller, 1774, by monotypy – synonym of *Leucochroa* Beck, 1837; Hygromiidae.)

Zenobia of authors. (Not *Zenobia* of Gray, 1821, type species *Helix (Zenobia) binarginata* Gray, 1821 = *Helix carthusiana* Müller, 1774, by monotypy – synonym of *Zenobiella* Gude & Woodward, 1921; Hygromiidae. Not of von Oken, 1815–16; Lepidoptera.)

Theba of authors. (Not *Theba* of Risso, 1826, type species *Helix pisana* Müller, 1774, designated by Gray (1847); Helicidae.)

Helicopsis of authors. (Not *Helicopsis* of Fitzinger, 1833, type species *Helix striata* Müller, 1774, by monotypy; Hygromiidae.) (Not of Fabricus, 1808; Lepidoptera.)

Xerophila of authors. (Not *Xerophila* of Held, 1838 (1837–38), type species *Helix pisana* Müller, 1774 = *Theba pisana* (Müller, 1774), designated by Herrmannsen (1847); Helicidae.)

Heliomanes of authors. (Not *Heliomanes* of Brown, 1840 (1837–49), listed in synonymy of *Cernuella* Schlüter, 1838, Hygromiidae, by Zilch (1959–60), type designation not traced. Not of Newman, 1840; Coleoptera.)

Candidula Kobelt, 1871: 22, type species *Glischrus (Helix) candidula* Studer, 1820 = *Helix unifasciata* Poiret, 1801, by monotypy.

Striatinella of authors. (Not *Striatinella* of Clessin, 1876 (1876–77), type species *Glischrus (Helix) candidula* Studer, 1820 = *Helix unifasciata* Poiret, 1801, source of designation not traced – synonym of *Helicopsis* Fitzinger, 1833; Hygromiidae.)

Xerovaga di Maria di Monterosato, 1892: 22, for *H. caperata*, *heripensis*, *gigaxii*, *andalusica*, type apparently not subsequently designated.

Xeroplexa of authors. (Not *Xeroplexa* of di Maria di Monterosato, 1892, type species *Helix setubalensis* Pfeiffer, 1850, designated by Kobelt (1892); Hygromiidae.)

Diagnosis. Shell globose to moderately depressed, umbilicate, pale-coloured, often with dark spiral bands; sculpture weak, radial. Genital orifice sited behind right ocular peduncle, at about 0.3 of distance posteriad towards pneumostome. Female genitalia with 2 stylophores on one side of vagina, one of them large and externally evident, the other vestigial and invisible. Proximal phallus a simple

tube penetrated by shaft of vergic papilla, the latter not joined to distal phallus wall by frenula. Right ocular retractor not crossing between phallus and vagina.

Haploid chromosome number 26 or 27.

Remarks. Chiefly western European in distribution.

Candidula intersecta (Poiret)

Figures 39, 79, 101, 120, 149, 175, 201, 228, C12, M17, M64, M65; Map 12

itala of authors (not of Linnaeus, 1758).
? *fasciolata* Poiret, 1801: 79 (*Helix*).
intersecta Poiret, 1801: 81 (*Helix*).
striata Draparnaud, 1801: 91 (in part) (not of Müller, 1774) (*Helix*).
caperata Montagu, 1803: 430 (in part) (*Helix*).
ignota Mabille, 1865: 255 (*Helix*).
paladilhi Bourguignat, 1866 (1863–70): 180 (*Helix*).
herbarum Servain, 1880: 92 (*Helix*).
carcusiaca Mabille, 1881: 123 (*Helix*).
deferiana Bourguignat, in Locard, 1882: 107, 332 (*Helix*).
subintersecta Bourguignat, in Locard, 1882: 113 (*Helix*).
pictonum Bourguignat, in Locard, 1882: 338 (*Helix*).
scabiosula Locard, 1899: 87 (*Helix*).
expedenta Locard, 1899: 113 (*Helix*).
imula Locard, 1899: 113 (*Helix*).

Shell (Fig. 39) small, subglobose, up to 8 mm high by 13 mm in diameter, perforate, of 5–6.5 slightly convex whorls with shallow sutures, slightly angled at the periphery, opaque, coloured buff to pale brown with dark brown to black irregular blotches; sculpture of coarse radial wrinkles and ribs. Umbilicus moderately wide, 0.14–0.17 of shell width. Protoconch (Fig. M17) of 1.25 whorls, smooth but for weak growth lines. Aperture ovate-lunate. Lower lip reflected, with an internal white rib set back from edge.

Animal grey, paling towards tail and foot margin, speckled white in head region; foot fringe below pedal groove strongly speckled grey; sole densely speckled grey towards lateral margins; mantle collar with grey margin. Active animal with tail not extending behind shell. Locomotion by muscular pedal waves generated from posterior of sole.

Reproductive system, Fig. 79. Ovotestis embedded in posterior lobe of digestive gland. Hermaprodite duct long, contorted and distended for much of its length, ending at base of albumen gland with a small diverticulate talon. Albumen gland large, linguiform. Spermoviduct moderately long; female tract sacculate, folded; male part with prostatic follicles distributed as a broad ribbon along entire length. Free oviduct very short, stout. Bursa copulatrix reservoir a large oval sac on a moderately long duct which generally broadens towards its origin in oviduct. Vagina large, bearing proximally paired mucus glands above a well developed, bulbous stylophore which opens towards atrium with a single protruding dart; dart about 2 mm long, straight or slightly curved, rounded in cross-section, narrowing from base embedded in stylophore wall to a fine point; mucus glands with 3 or 4 tubular, sometimes branched, finger-like processes arising from a very short, sacculate stem; internal wall of vagina opposite stylophore carrying a longitudinally folded stimulatory shield, with vestiges of a second, unarmed stylophore sac. Vas deferens long, slender, terminating in epiphallus lateral to its short apical flagellum. Epiphallus about 3x as long as phallus, cylindrical. Phallus saccular, broader than epiphallus, covered with a thin muscular sheath which extends over vagina and stylophore; a large, elongate, conical epiphallic papilla occupying most of the internal space; lumen wall with minute papillae, spinose in proximal part. Atrium very short.

Spermatophore (Fig. 101) about 9 mm long, slender, narrowing to bluntly pointed extremities, bearing a longitudinal spiralled ridge which is ornate, with a double row of spines in its middle section.

Phallus retractor arising from diaphragm about midway along pulmonary cavity, inserted on epiphallus at about 0.65 from its proximal end.

Jaw (Fig. 120) 0.8 mm wide, weakly ribbed, with anterior margin strongly concave, the lateral extremities broadly rounded and projecting anteriorly.

Radular ribbon (Fig. M64, 65) with 95–102 transverse rows of teeth, each row varying about the formula 14+9+C +9+14. Central tooth tricuspid, on a quadrate basal plate, with a prominent, rather broad mesocone and small, pointed ectocones. Lateral teeth bicuspid, on quadrate basal plates, with a large mesocone and a short but prominent ectocone. Marginal teeth on reduced but broad basal plates, with mesocone and ectocone retained, tending to become serrate towards radular margin.

Digestive tract, Fig. 149. Buccal mass spheroidal. Oesophagus short. Crop occupying about 1.2 whorls, divided by a medial constriction into a cylindrical oesophageal part and a more sacculate gastric part. Stomach sacculate, not externally differentiated from gastric crop. Intestine producing a short anteriorly directed loop to abut the kidney, then reflected to a short posteriorly directed loop, before running forwards to anus in mantle collar.

Pallial complex, Fig. 175. Pulmonary cavity about 3x longer than wide. Kidney triangular, extending from posterior of pulmonary cavity to about 0.3 of its length. Ureter sigmoid, its primary arm along anterior of kidney closed, opening at posterior of pulmonary cavity into a

ureteric gutter which extends adjacent to rectum to the mantle collar. Pericardium applied to left side of kidney. Pulmonary vein well developed, but vascularisation of mantle rather weak.

Free muscle system, Fig. 201. Left tentacular and buccal retractors arising from a short common stem with origin on columella. Buccal retractor a broad sheet anteriorly, not bifurcating before its insertion on buccal mass. Right tentacular retractor a separate branch from its origin, not passing over phallus to its insertion in ocular peduncle and inferior tentacle.

Central nervous system, Fig. 228. Cerebral commissure short, less than half cerebral ganglion width. Left cerebro-pedal connective slightly longer than the right, its length about twice width of cerebral ganglion. Pleural ganglia closer to pedal ganglia than to cerebral ganglia, closely appressed to parietal ganglia. Visceral ganglion fused to left parietal ganglion and closely appressed to right parietal ganglion, lying to left of median plane.

Haploid chromosome number 26.

Type material. Described in a paper on species in the environs of Paris, without a precise type locality. The whereabouts of the type material is unknown; presumably it is lost.

Distribution. The native range is Western Europe, from the British Isles, western and northern France, Belgium, and The Netherlands, to scattered localities in Portugal, Germany, Denmark, and southern Sweden. Introduced into Australia and New Zealand.

Recommended common name. Wrinkled snail.

Material examined. New Zealand. ND. Spirits Bay, May 1985, P.C. Mayhill. Tauputoputo, 8 May 1972, B. Penniket; 13 Nov 1979 and 6 Jul 1993, B.F. Hazelwood, in sand dunes. **CL.** Waikawau, Freyberg (MONZ). **WO.** Waipapa, Waitomo, 1970–72, S. Easterbrook-Smith (MONZ M39127). Waitomo, 23 Apr 1978, in scrub on limestone outcrop. Mahoenui Valley, Totara Rd cave, 5 Mar 1977, F.M. Climo (MONZ M56847). **BP.** Mt Maunganui, 5 Jul 1966, N.J. Peterson (MONZ M76618). Papamoa Beach, Sep 1989, Jun 1991, May 1992, in sand dunes. **GB.** Wainui Beach, Jan 1976, G.A. Foreman. Gisborne, 1981, C. Broomfield (MONZ M69532). **RI.** Kereru, Feb 1981, P.C. Mayhill. **HB.** Tangoio, 25 Feb 1968, D.J. Roscoe (MONZ M89486). Eskdale, 24 Aug 1958, R.K. Dell (MONZ M13271). Napier, 23 Jul 1967, D.J. Roscoe (MONZ M47008). Te Mata, 2 Apr 1967, D.J. Roscoe (MONZ M46931); 14 Aug 1976, B.F. Hazelwood (MONZ M52247). Havelock North, F. Duguid (MONZ M62359). Havelock North, Webb's Bush, Sep 1979, P.C. Mayhill; 1981, C. Broomfield (MONZ M69531). Maraetotara, Jun 1955, W.H. Hartree (MONZ); 14 Aug 1976, B.F. Hazelwood & H.B. Hazelwood (MONZ M52338).

Maraetotara Gorge Reserve, 14 Aug 1976, B.F. Hazelwood (MONZ M69130). Waimarama Gorge, 14 Aug 1976, B.F. Hazelwood (MONZ M52336). **WI.** Wanganui, Castlecliff, B.F. Hazelwood. **WN.** Rawiti, 1962, F. Duguid (MONZ M54170). Waikarere Beach, 2 Jun 1963, R.G. Ordish (MONZ M25408). Otaki, 24 Dec 1979, 20 Apr 1980 and 26 Oct 1981, B.F. Hazelwood (MONZ M63086, M68786, M70439). Pukerua Bay, Feb 1988, L. Hayes (MONZ M89849). Porirua, 1957, A.G. Beu (MONZ M32021). Wellington, Seatoun, 1922, W.R.B. Oliver (MONZ M13274). Petone, 4 Oct 1959, A.G. Beu (MONZ M32020). Rona Bay, 1958, A.G. Beu (MONZ M32022). Worser Bay, 1938, O'Connor (MONZ). Wellington, 25 Jul 1953, R.A. Falla (MONZ). Wellington, Epuni, 1959, A.G. Beu (MONZ M32019). Evans Bay, 2 Aug 1979, F.M. Climo (MONZ M77227). Lyall Bay, 22 Jun 1949, R.K. Dell (MONZ). **WA.** Aohanga, 8 Mar 1937, C.A. Fleming (MONZ M84658). Castlepoint, May 1950, J.H. Sorensen (MONZ M28961); 1 Feb 1963, R.K. Dell (MONZ M16499); 23 Dec 1976, G.K. Eastop (MONZ M84659); Apr 1991, P.C. Mayhill. Mauriceville, 28–29 Aug 1969, S. Markham (MONZ M31064, M31067); undated, F. Hutchinson (MONZ M22067). Riverdale, Mar 1971 (MONZ M69535). Uruti Beach, 19 Dec 1971 (MONZ M69536). Gladstone, Jul 1953, P.C. Bull (MONZ). Flat Point, 1973, B. McFadgen (MONZ M48632). Ruakokopatuna Cave, 3 Mar 1952, J.C. Yaldwyn (MONZ); 1966, O.J. Marston, Harrison's Hole *ca* 2000 ft (MONZ M47516); 6 Jan 1969 – 15 Jan 1970, S. Markham (MONZ M30191). Ruakokopatuna, 10 Jul 1977 and 18 Dec 1982, B.F. Hazelwood (MONZ M75662, M75812, M76850). Cape Palliser, 5 Jan 1991, in sand dunes. **KA.** Kaikoura Peninsula, South Bay, 16 Feb 1975, M. Efford (MONZ M69709). **MC.** Castle Hill, Cave Stream, Jan 1992, P.C. Mayhill. **SC.** Pareora, Jan 1974, H. Goldson. Esk Valley, 7 Sep 1969 (MONZ M69533). Hunter Hills, 21 Sep 1991, L. Ford. Waihao Forks, Jan 1974, H. Goldson. Bortons, 21 Sep 1991, L. Ford. **SI.** Halfmoon Bay, undated, E.C. Smith (MONZ M30512).

Extralimital. England. Liverpool, Merseyside, 1977, coll. & det. N. McMillan. **Wales.** Oxwich, West Glamorgan, Jul 1965, coll. & det. R.A.D. Cameron.

History in New Zealand. The first record of *C. intersecta* in New Zealand is that of Suter (1891) for a colony at Nelson. Suter (1913) lists Paekakariki and Nelson as localities. Moore (1952) added Waikawau (Thames coast), and Whitten (1955, 1957) added several southern North Island localities. Powell (1979) indicated that *C. intersecta* was "now widespread in both North and South Islands but less common in the north."

According to Taylor (1921 (1902–21)), F.W. Watton recorded *Helicella itala* (Linnaeus, 1758) from Wellington in 1892, said to have been imported five or six years earlier with English grass seed. *H. itala* had established in York Peninsula, South Australia at about the same time, apparently also via importation of grass seed (Taylor 1921 (1902–21)). Taylor commented that the Wellington shells closely resembled those established in South Australia, which in turn he likened to a further European species, *H.*

obvia (Menke, 1828). As neither *H. itala* nor *H. obvia* is known from the Wellington region or anywhere else in New Zealand, it would seem that Taylor misidentified the material collected by Watton. *C. intersecta* is common in the Wellington area, and I refer Taylor's records to this species. Quick (1952) perpetuated the Wellington records of *H. itala* without examining any material from New Zealand.

Biology. *C. intersecta* is regarded as an 'open country' species in Europe (e.g., Chatfield 1975, Kerney & Cameron 1979, Rouse & Evans 1994). In New Zealand it is found in open, dry habitats such as coastal dunes, exposed limestone outcrops, open scrub, and pasture. It ranges from sea level to over 800 m in altitude. During dry weather the snails bury themselves.

Remarks. In Europe, *C. intersecta* may be readily confused conchologically with several other *Candidula* species, especially *C. belemensis* (Servain, 1880), *C. gigaxii* (Pfeiffer, 1848) and *C. unifasciata* (Poiret, 1801), and with unrelated hygromiid species such as *Trochoidea geyeri* (Soós, 1926).

Germain (1930), Backhuys (1975), and Gittenberger (1993b) provide an introduction into the European literature on *C. intersecta*.

Genus *Prietocella* Schileyko & Menkhorst

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Bulimus of authors. (Not *Bulimus* of Scopoli, 1786 (1786–88), type species *Bulimus haemastomus* Linnaeus, 1758, designated by Gray (1847) – synonym of *Megalobulimus* Miller, 1878; Acavidae.)

Helicella of authors. (Not *Helicella* of d'Audebard de Férussac, 1821, type species *Helix ericetorum* Müller, 1774 = *Helicella itala* (Linnaeus, 1758), designated by Herrmannsen (1847) – ICZN Opinion 431 (1956: 350); Hygromiidae.)

Cochlicella of authors. (Not *Cochlicella* of d'Audebard de Férussac, 1821, type species *Helix conoidea* Draparnaud, 1801, designated by Gray (1847) – ICZN Opinion 335 (1955a: 48, 56; Hygromiidae.)

Xerophila of authors (Not *Xerophila* of Held, 1838 (1837–38), type species *Helix pisana* Müller, 1774 = *Theba pisana* (Müller, 1774), designated by Herrmannsen (1847) – synonym of *Theba* Risso, 1826; Helicidae.)

Xeroacuta of authors. (Not *Xeroacuta* of di Maria di Monterosato, 1892, type species *Helix cretica* Pfeiffer, 1841, designated by Kobelt (1892) – synonym of *Xerocrassa* di Maria di Monterosato, 1892; Hygromiidae.)

Prietocella Schileyko & Monkhorst, 1997: 54, type species

Helix barbara Linnaeus, 1758, by original designation and monotypy.

Diagnosis. Shell small, more or less turriform or conical, higher than wide, narrowly umbilicate, varying from opaque white with brown bands or flecks to largely corneous with opaque white streaks; aperture small, the lip thin and simple, reflected at columellar margin. Genital orifice immediately posterior to right ocular peduncle. Stylophore bearing apical mucus glands, opening into atrium. Bursa copulatrix duct unbranched. Epiphallus with a small flagellum.

Haploid chromosome number 23.

Remarks. *Prietocella* comprises three European species, one of which has established in New Zealand.

Prietocella barbara (Linnaeus)

Figures 40, 80, 102, 121, 150, 176, 202, 229, C13, M18, M66–68, M117, M118; Map 13

barbara Linnaeus, 1758: 773 (in part) (*Helix*).
acuta of authors (not of Müller, 1774).
ventricosus Draparnaud, 1801: 68 (not of Bruguière, 1791 (1789–1816); Bradybaenidae) (*Bulimus*).
ventrosa d'Audebard de Férussac, 1821: 56 (new name for *Helix ventricosa* Draparnaud, 1801) (*Helix* (*Cochlicella*)).
bulimoides Moquin-Tandon, 1855: 277 (*Helix* (*Cochlicella*)).

Shell (Fig. 40) high conic, up to 12 mm high by 5 mm in diameter, of 6–7.5 thin whorls, perforate with umbilicus minute, pale brown, generally profusely streaked and flecked with opaque buff, but this pattern often lacking, especially on body whorl; body whorl often with a brown band; surface slightly glossy; growth lines rather distinct, especially immediately below suture. Protoconch (Fig. M18) of 1 whorl, its surface irregularly pitted and with microscopic striae. Aperture rounded-oval, the lip thin. Columella erect, reflected.

Animal densely speckled grey-brown dorsally, sparsely speckled grey at sides of foot; sole off-white or pale grey; mantle collar speckled grey towards anterior margin. Genital orifice a little posteriad of right peduncle.

Reproductive system, Fig. 80. Ovotestis embedded in posterior lobe of digestive gland, comprising 3 progressively larger clusters of acini along first part of hermaphrodite duct. Hermaphrodite duct only briefly slender, for the greater part distended and highly convoluted, but straightening to end in talon at base of large albumen gland. Spermoviduct of moderate length; female part much folded; male part a broad ribbon of prostatic follicles extending full length of duct. Free oviduct short, broad-

ening towards duct of bursa copulatrix. Bursa copulatrix duct long, broad and thick-walled for 0.2 of its length from origin in oviduct, remainder thin-walled with saccular terminal and subterminal distensions. Vagina short, stout. Vas deferens long, slender, inserted in epiphallus at base of short flagellum. Epiphallus long, cylindrical, somewhat contorted proximally, internally with longitudinal folds; entry into phallus with a long vergic papilla capped by a nodulose pad. Phallus short, bulbous, occupied for the most part by vergic papilla; internal lining smooth. Atrium short, carrying opposite phallus a sacculate stylophore upon which issue 4–6 slender, tubular mucus glands.

Spermatophore (Fig. 102) 1.75 mm long, slender, slightly spirally twisted, tapered to a point at both ends, ornamented with 2 serrate ridges.

Phallus retractor arising from diaphragm, inserted on epiphallus a little proximal of junction with phallus.

Jaw (Fig. 121) about 0.8 mm wide, with anterior margin strongly concave, irregularly ribbed.

Radular ribbon (Fig. M66–68) with 93–100 transverse rows of teeth, each row varying about the formula 8+10+ C+10+8. Central tooth tricuspid, on a quadrate basal plate, with a prominent, rather broad mesocone and small, weakly pointed ectocones. Lateral teeth bicuspid, on quadrate basal plates, with a large mesocone and short but prominent ectocone. Marginal teeth on reduced but broad basal plates, with mesocone and ectocone retained, tending to become serrate towards radular margin.

Digestive tract, Fig. 150. Buccal mass spherical. Oesophagus short, expanding abruptly into a long, cylindrical crop which grades imperceptibly into stomach. Intestine long, from stomach forming an anteriorly directed loop abutting kidney, then turning back in a posteriorly directed loop before making a complete whorl anteriorly to reach anus in mantle collar.

Pallial complex, Fig. 176. Pulmonary cavity long and slender, extending about 0.9 of body whorl in active animal. Kidney triangular, its greatest dimension in wall abutting pericardium on left. Ureter sigmoid, closed in primary part along anterior margin of kidney, but an open channel for greater part of its course adjacent to rectum. Primary vein on pulmonary cavity roof strongly developed, but secondary vascularisation poor.

Free muscle system, Fig. 202. Columellar muscle system strongly developed, arising as a single stem, dividing sequentially into right tentacular retractor, tail fan, left tentacular retractor, and buccal branches. Right ocular retractor dividing shortly after origin to form 3 branches, to ocular peduncle, inferior tentacle, and antero-lateral body wall and female genitalia, passing forward inside atrium and not crossing phallus. Tail fan extensively branched to anterior pedal area and lateral body wall, sending separate branches to left ocular peduncle and left inferior tentacle.

Central nervous system, Fig. 229. Cerebral commissure length about half cerebral ganglion width. Left cerebro-pedal connective slightly longer than the right, its length about 1.5x cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia, the left closely appressed to left parietal ganglion, the right apparently fused to right parietal ganglion. Visceral ganglion fused to left parietal ganglion and closely appressed to right parietal ganglion, lying to right of median plane.

Haploid chromosome number 23.

Type material. No type locality was given by Linnaeus (1758). The whereabouts of the type material is unknown; presumably it is lost.

Distribution. Native to the Mediterranean region. Introduced to North America, Bermuda, South Africa, Australia, and New Zealand.

Recommended common name. Banded conical snail.

Material examined. New Zealand. ND. Tauputoputo Bay, 13 Nov 1979 and 6 Jul 1993, B.F. Hazelwood. Taipa, 16 Jul 1992, O.J. Marsten, in sand dunes. Bland Bay, 17 Feb 1989, B.F. Hazelwood & S. O'Shea, in sand dunes. Whangaruru, 17 Feb 1989, B.F. Hazelwood, coastal cliff. **AK.** Tapora, Apr 1983, D. Armstrong, in lucerne; May 1983, R. Kleinpaste; Jul 1983, in lucerne, R. Kleinpaste (MONZ M78692). Port Albert, Oct 1992, N. Gardner. Kiwitehere, Oct 1985, A.B. Grace (MONZ M82922). Wellsford, 1982, R. Kleinpaste (MONZ); 17 Jul 1988, J.F. Goulstone. Te Hana, 31 Oct 1993, 10 Jan 1994 and 23 Feb 1994, in pasture.

Extralimital. Australia. York Peninsula, South Australia, Sep 1988, in pasture. **England.** Torquay, Aug 1990, coastal garden.

History in New Zealand. *P. barbara* was first discovered in New Zealand on farmland at Tapora, south-west of Wellsford, in May 1983. Surveys by staff of the Ministry of Agriculture and Fisheries revealed it to be well established at that time in the Tapora area, with population densities as high as 600 per m^2 in lucerne fields (R. Kleinpaste, pers. comm.). This is the first formal record of the species in New Zealand. The species is now widely distributed in Northland and north Auckland.

Biology. The habitat of *P. barbara* in its native range is, according to Kerney & Cameron (1979, p. 184), "dry exposed sites near the sea, especially dunes, occasionally inland in S. France." The habitat in New Zealand agrees closely, the species becoming increasingly more widespread and abundant on coastal dunes and in summer-dry pastures in Northland.

P. barbara is frequently present in large numbers, as indicated above. More recent surveys (1992–95) by this author indicate that abundance varies markedly between sites, even where the snail has been established for more than 5 years. In the Te Hana and Hakaru areas, for example, populations in pasture vary from 2 per m^2 to in excess of 1000 per m^2. The snails feed on both living and decaying plant material. There have been no reports of damage to lucerne or pasture.

These snails are very tolerant of dry conditions, though in extremes they seal the aperture of the shell with an a series of epiphragms to prevent moisture loss. The first-formed, outer epiphragm frequently incorporates, or has adhering to it, small fragments of plant litter.

Eggs (Fig. M117, 118) are 1.0x1.2 mm, with a flexible shell comprising numerous calcite crystals embedded in a jelly layer.

Remarks. Germain (1930), Giusti (1970, 1976), and Forcart (1976) provide an introduction into the European literature on *P. barbara*.

Family LIMACIDAE

Diagnosis. Large aulacopod slugs, primarily herbivorous, with a rudimentary, internalised shell. Body elongate, tapering posteriorly; keel varying in length, sometimes reaching posterior margin of mantle shield. Mantle less than half of body length, situated in anterior part of body. Pneumostome usually in posterior right margin of mantle, exceptionally in anterior right margin. Sole divided into 3 longitudinal zones, with transverse grooves. Suprapedal gland embedded in foot tissues. Kidney approximately oval, without any lobe, partially enclosing heart on right side; secondary ureter separated from kidney, terminating in urinary bladder. Cephalic retractors arising near body midline, a little posterior to pallial complex. Buccal mass spheroidal. Jaw oxygnathic. Radula with marginal teeth dagger-like or sword-like. Intestine with 2 anteriorly directed loops. Right ocular retractor crossing phallus or free of genitalia. Genital orifice immediately behind right ocular peduncle, or posteriad from peduncle about 0.3 of distance to pneumostome. Male and female pallial gonoducts united as spermoviduct. Oviduct and atrium without accessory glands. Epiphallus absent; spermatophores not produced. Phallus with stimulatory folds. Central nervous system with cerebropedal connectives equal in length and rather short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 24–31.

Remarks. This taxon has recently been raised to family rank, distinguishing it from the agriolimacid slugs (Likharev & Wiktor 1980, Wiktor & Likharev 1979, 1980). Limacid slugs occur naturally in North Africa, Europe, the Caucasus, Central Asia, and Asia Minor. Included genera are *Limax* Linnaeus, 1758, *Lehmannia* Heynemann, 1862, *Malacolimax* Malm, 1868, *Limacus* Lehmann, 1864, *Eumilax* Boettger, 1881, *Gigantomilax* Boettger, 1883, *Bielzia* Clessin, 1887, *Metalimax* Simroth, 1896, *Turcomilax* Simroth, 1901, *Caspilimax* Hesse, 1926, and *Caucasolimax* Likharev & Wiktor, 1980. Several species of *Limax* and *Lehmannia*, and the sole species of *Limacus*, have been widely distributed through the activities of man.

Genus *Lehmannia* Heynemann

Lehmannia Heynemann, 1862: 211, type species *Limax marginatus* Müller, 1774, by original designation.

Agriolimax of authors. (Not *Agriolimax* of Mörch, 1865, type species *Limax agrestis* Linnaeus, 1758, designated by Malm (1868); Agriolimacidae.)

Malacolimax of authors. (Not *Malacolimax* of Malm, 1868, type species *Limax tenellus* Müller, 1774, according to Hesse (1926); Limacidae.)

Eulimax of authors. (Not *Eulimax* of of Moquin-Tandon, 1855, type species *Limax maximus* Linnaeus, 1758, designated by Pilsbry (1922) – synonym of *Limax* Linnaeus, 1758; Limacidae.)

Simrothia Clessin, 1884 (1884–85): 62, listed in synonymy by Wiktor (1973), type designation not traced.

Ambigolimax Pollonera, 1887a: 1, type species *Limax valentianus* d'Audebard de Férussac, 1823, by monotypy.

Mesolimax of authors. (Not *Mesolimax* of Pollonera, 1888, type species *Mesolimax brauni* Pollonera, 1888, by monotypy; Agriolimacidae.)

Melitolimax Pollonera, 1891: 4, type species *Limax melitensis* Lessona & Pollonera, 1882, designated by Hesse (1926).

Diagnosis. Shell internal, an asymmetrical, broadly oval plate with concentric growth lines radiating from vestigial protoconch at left posterior margin. Keel of posterior body short and ill defined. Pneumostome in right posterior part of mantle. Mantle shield with concentric ridges, their nucleus lying in mid-dorsal line. Jaw oxygnathic, with a medial projection. Right ocular retractor crossing over phallus. Phallus short, cylindrical to club-shaped, often with a whip-like apical caecum, always with a well developed retractor. Bursa copulatrix duct connected to distal phallus. Prostatic gland fused to oviduct for its entire length. Vas deferens well developed. Vagina absent. Rectal caecum always present, extending to posterior of body cavity. Genital orifice immediately behind and below right ocular peduncle.

Haploid chromosome number 24.

Remarks. European and North African slugs, mostly of forested mountain areas. The genus contains 16 nominal species. Represented in New Zealand by two naturalised species.

Lehmannia nyctelia (Bourguignat)

Figures 41, 45, 81, 122, 151, 177, 203, 230, C14, C15, M69–72; Map 14

marginata of authors (not of Müller, 1774).
arborum of authors (not of Bouchard-Chantereaux, 1837).
nyctelius Bourguignat, 1861: 305 (*Limax*).
legrandi Tate, 1881: 16 (*Limax*).
brauni Babor, 1898: 41 (*Mesolimax*).
kervillei Germain, 1907: 154 (*Agriolimax* (*Malacolimax*)).

Extended animal (Fig. 41a–c) 40–60 mm long, with an ill defined keel at hind end. Mantle about 0.35 of body length. Body pale greyish yellow to greyish chocolate brown. Mantle with lateral bands and diffuse central band of dark brown or black; border around pneumostome pale. Back with a pale medial zone, sides with 1 or 2 pairs of more or less visible bands of brown or black, these sometimes broken up into spots or entirely lacking. Sole uniformly creamy-grey. Mucus clear. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 45) white and irridescent, oblong-oval, up to 7x4.8 mm, varying in degree of calcification and thus irregular in thickness and outline. Dorsal surface convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, usually not protruding, situated centrally or asymmetrically at left. Organic sheet surrounding the shell, usually extending well beyond calcified part.

Reproductive system, Fig. 81. Ovotestis small, deeply pigmented, exposed dorsally between lobes of digestive gland near posterior of body cavity. Hermaphrodite duct initially straight, then convoluted and swollen, with pale talon near large, ovate albumen gland. Spermoviduct folded, dominated by female tract proximally. Free oviduct of moderate length, often slender. Vagina absent. Vas deferens short, running directly from origin in prostatic gland to phallus apex, adjacent to insertion of phallus retractor. Phallus cylindrical, often somewhat folded, inflated at proximal apex, internally with 2 prominent folds. Bursa copulatrix reservoir large, oval, on a short duct opening to phallus near atrium.

Phallus retractor short, arising from diaphragm at left lateral margin of kidney.

Jaw (Fig. 122) 1.8–2.0 mm wide, with a medial projection and transversely scored with fine striae.

Radula (Fig. M69–72) with about 106 tranverse rows of teeth, each with a formula varying around 43+30+C+30+43. Central tooth tricuspid, with mesocone prominent, flanked on either side by small ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by small but well defined endocone and ectocone. Mesocone progressively more slender and elongate on lateral teeth, without accessory cusps, and then on marginal teeth shorter and serrate-edged.

Digestive tract, Fig. 151. Buccal mass spheroidal. Oesophagus expanding to large crop, extending to 0.6–0.7 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach to run forwards and over anterior aortic branch, then producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor, then forming a further short, posteriorly directed loop and running forwards to anus; rectal caecum arising from last intestinal loop, running along right side to posterior of body cavity.

Pallial complex (Fig. 177) located in posterior of mantle. Kidney bean-shaped, with long axis oblique to body axis, partially enclosing heart on its left anterior side. Secondary ureter separating from kidney at left posterior and describing an arc to right anterior part of pallial complex, where it inflates to form a urinary bladder. Heart ventricle producing a long aortic stem directed posteriorly and to the right. Lung heavily vascularised.

Free muscle system, Fig. 203. Cephalic retractor attached on dorsal body wall a little posterior to pallial complex, and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising as a branch from stem or from left tentacle retractor; second anterior loop of intestine passing over cephalic retractor muscle stem near its origin.

Central nervous system, Fig. 230. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia, closely appressed to parietal ganglia. Visceral chain compact, but pleural, parietal, and visceral ganglia distinct; visceral ganglion to right of median plane.

Chromosome number unknown.

Type material. Bourguignat's original material was collected from Algiers; its whereabouts are unknown, and it is presumed lost.

Distribution. *L. nyctelia* occurs in natural environments in the Balkans and in the mountains of eastern and central Europe, indicating that it is probably native there (Wiktor

1982, 1983a). On the basis of ecological requirements, the presence of *L. nyctelia* in North Africa has been attributed to introduction through the activities of man. According to Grossu & Lupu (1965) the species was originally distributed over a large area, including the Mediterranean region, while its present distribution is relict. As a synanthrope it has been introduced into Europe, North America, South Africa, Great Britain, Egypt, Australia, and New Zealand.

Recommended common name. Bourguignat's slug.

Material examined. New Zealand. ND. Motuekaiti I., 21 Apr 1993, Parrish. **AK**. Henderson, 6 Jul 1991, F.T. Graham, in garden. Titirangi, Oct 1979, in nursery, associated with potting plants. **WO**. Tauwhare, 3 Jan 1996, in pasture. Matangi, Whewell's Bush, 14 Jan 1996, in *Podocarpus dacrydioides* forest remnant. Hamilton, 4 Sep 1977, P.C. Mayhill, in garden; 11 Aug 1992, in gardens and pasture. Newstead, 2 Nov 1993, in pasture. **BP**. Katikati, 11 Sep 1993, in garden. Opotiki, 12 Sep 1986, in dunes. **WI**. Turakina, 26 Sep 1981, S. Staple. **WN**. Levin, 20 Nov 1991, J.S. Smith, in garden. **NN**. Mapua, 29 Nov 1977 and 3 Jan 1978, J. Marris; 1 Mar 1978, J. Collard; 24 Apr 1978, W.K. Marris.

Extralimital. Australia. Albury, New South Wales, 14 May 1992, under timber at roadside.

History in New Zealand. *L. nyctelia* was first reported in New Zealand by Barker (1979) on the basis of material collected at Hamilton and Mapua during 1977. Because of the apparent restricted distribution, Barker (1979, 1992) suggested that *L. nyctelia* had established in New Zealand relatively recently, probably during the latter part of the 1970s in association with imported of plant material. This concept is supported by the current situation, with (i) an apparently very restricted distribution, largely confined to urban areas, and (ii) populations at establishment sites still in a phase of rapid increase and local dispersal.

However, the species may have established considerably earlier. *L. marginata* Müller, 1774 (as *Limax arborum* Bouchard-Chantereaux, 1837) was recorded from New Zealand and Australia by Taylor (1902–07 (1902–21)) on the basis of specimens collected in 1905 by W.D. Roebuck and associates. These records were repeated in subsequent literature without critical review (e.g., Quick 1949, 1960, Cotton 1954, Burch 1960), although Quick (1960) did examine specimens from Australia. Van Regteren Altena & Smith (1975) considered Taylor's Australian records of *L. marginata* to be misidentifications, with the material referable to the widespread naturalised *L. nyctelia*.

It is possible that Taylor also misidentified New Zealand *L. nyctelia*, but confirmation of this can only be obtained through examination of the material that Taylor had before him. To date no *Lehmannia* has been collected from Wellington, the source of Taylor's New Zealand

material. It is also possible that a population of *L. marginata* had established in Wellington around the turn of the century but subsequently perished. The situation is further complicated by the fact that many records of *L. marginata* or *L. arborum* have proved to be referable to *L. valentiana* d'Audebard de Férussac, 1823 (Waldén 1961), a species also now established in New Zealand.

I confirm my earlier proposal (Barker 1979) that *L. marginata* be withdrawn from the New Zealand list of naturalised molluscs until such time as its presence is confirmed by collection and accurate identification of fresh material.

Biology. The natural habitat of *L. nyctelia* in Europe is mountainous deciduous forests and subalpine herbfields, where it feeds mainly on lichens upon rocks and trees (Wiktor 1983a). In New Zealand this species is at present known only from within nurseries and domestic gardens, or areas immediately surrounding them. It is found under rocks, logs, pots, and planter trays and around the roots of plants, and can occur in high numbers, inflicting significant damage on some cultivated plants.

Mating and egg laying have not been observed in New Zealand, though translucent yellow eggs have been found in spring, measuring 2x1.5 mm to 2.3x1.6 mm.

Remarks. Dissections are required to separate *L. nyctelia* from *L. valentiana*.

An introduction to the literature on *L. nyctelia* is provided by Quick (1960), Grossu & Lupu (1965), van Regteren Altena (1966), Wiktor (1967, 1973, 1983a, 1989), Giusti (1976), and Likharev & Wiktor (1980).

Lehmannia valentiana (d'Audebard de Férussac)

Figures 42, 46, 82, 123, 152, 178, 204, 231,C16, M73–76; Map 15

marginatus of authors (not of Müller, 1774).
valentianus d'Audebard de Férussac, 1823 *in* d'Audebard de Férussac & Deshayes, 1820–51: 96 (*Limax*).
arborum of authors (not of Bouchard-Chantereaux, 1837).
poirieri Mabille, 1883: 52 (*Limax*).
getica Grossu, 1970: 109 (*Lehmannia*).

Animal (Fig. 42a–c) 60–75 mm when extended, with an ill defined keel at hind end. Mantle about 0.35 of body length. Body pale greyish yellow, brown, or red-brown. Mantle with a median band and 2 conspicuous lateral bands; lateral and anterior margin spotted or mottled; border around pneumostome pale. Back usually with a pale medial zone flanked by a band on either side, and below these variously spotted or with diffuse lower bands. Bands on mantle and

body often broken into spots, or entirely lacking, or occasionally entire body with a mottled reticulated pattern. Bands, spots, and mottling brown. Sole uniformly creamy grey. Mucus clear. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 46) white and irridescent, oblong-oval, up to 7.5x5 mm, varying in degree of calcification and thus thickness. Dorsal surface convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, usually non-protruding, situated centrally or asymmetrically on left. An organic sheet surrounding the shell, usually extending a short distance beyond calcified part.

Reproductive system, Fig. 82. Ovotestis large, superficially pigmented, exposed dorsally between lobes of digestive gland adjacent to stomach. Hermaprodite duct initially straight, then convoluted and swollen, with pale talon near large, ovate albumen gland. Spermoviduct folded proximally. Free oviduct short, stout. Vagina absent. Bursa copulatrix reservoir on a moderately long duct to base of phallus. Vas deferens short, running directly from origin in prostatic gland to phallus apex. Phallus with a short cylindrical section arising from atrium, then bifid apically with one limb – the phallus apex proper – penetrated by vas deferens, the other a short cylindrical appendix; internally phallus with 2 prominent folds arising from base of appendix and extending, one further than the other, into distal section.

Phallus retractor short, arising from diaphragm at left lateral margin of kidney and inserted in middle part of phallus below bifurcation.

Jaw (Fig. 123) about 2.3 mm wide, transversely scored with fine striae and bearing a prominent medial projection.

Radula (Fig. M73–76) with 100–160 tranverse rows of teeth, each with a formula varying around 45+15+C+15+45. Central tooth tricuspid, with mesocone prominent, slender, flanked on either side by small ectocones. First lateral teeth tricuspid, with prominent mesocone flanked by small but well defined endocone and ectocone. Mesocone of lateral teeth progressively more slender and elongate, without accessory cusps in mature animals. Teeth progressively shorter towards radular margin; mesocone at first with a small accessory cusp, then serrate-edged.

Digestive tract, Fig. 152. Buccal mass spheroidal. Oesophagus expanding to large crop, extending to 0.6–0.7 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach to run forwards and over anterior aortic branch, then producing a posterior loop overlying crop, again running forwards to pass over stem of cephalic retractor, then forming a further short, posteriorly directed loop, and finally running forwards to anus; rectal caecum arising from last intestinal loop to run along right side to posterior of body cavity.

Pallial complex (Fig. 178) located in posterior of mantle. Kidney bean-shaped, with long axis oblique to body axis, partially enclosing heart on its left anterior side. Secondary ureter separating from kidney at left posterior and describing an arc to right anterior part of pallial complex, where it inflates to form a urinary bladder. Heart ventricle producing a long aortic stem directed posteriorly and to the right. Lung heavily vascularised.

Free muscle system, Fig. 204. Cephalic retractor arising as a bifid stem on dorsal body wall a little posterior to pallial complex, and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising as a branch from stem or from left tentacle retractor; second anterior loop of intestine passing over cephalic retractor muscle stem near its origin.

Central nervous system, Fig. 231. Cerebral ganglia united by a very short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact, but pleural, parietal, and visceral ganglia distinct; visceral ganglion to right of median plane.

Chromosome number unknown.

Type material. The type material, from Valencia, Spain, no longer exists.

Distribution. Native to the Mediterranean area, especially the Iberian Peninsula, and Atlantic islands. Carried by man to many parts of the world, including Europe, the Azores, the U.S.A., Colombia, Chile, Peru, Juan Fernandez, Easter Island, South Africa, Australia, and New Zealand.

Recommended common name. Valencia slug.

Material examined. New Zealand. AK. Titirangi, Oct 1979, in nursery, associated with trays and pots of native shrubs. Ellerslie, Oct 1979, 6 Mar 1980, 17 Jul 1992, 14 Sep 1993 and 28 Nov 1994, in greenhouses. **WO.** Port Waikato, Dec 1979, A.A. Kugler, in gardens. Hamilton, 8 Dec 1993, in gardens. **TK.** Ohangai, 7 Jul 1988, J.I. Townsend, in greenhouse, associated with orchids.

Extralimital. Australia. Gosford, New South Wales, June 1994, P. Colman. **Romania.** Bucurest, 9 Apr 1960, coll. & det. D. Lupu, in greenhouses. **South Africa.** Stellenbosch, Cape Province, 1978, coll. & det. W.F. Sirgel.

History in New Zealand. This is the first record of *L. valentiana* in New Zealand, with specimens first collected in Auckland and the northern Waikato during 1979. It is at present confined to a small number of localities in the

North Island, principally in association with greenhouse plants such as orchids. This is highly suggestive of recent introduction and establishment in New Zealand.

Biology. *L. valentiana* is strictly terrestrial and not arboreal, unlike several other *Lehmannia* species. From the material examined it is apparent that this species, living outdoors, reaches maturity during the New Zealand summer, with eggs present from late summer to early spring. Mature slugs and eggs were evident throughout the year in material from greenhouses. Mating was not witnessed during this study.

Webb (1961b, pp. 44, 46) describes mating in this species (as *L. marginata*) as follows. "Courtship commences when one slug begins to follow at the tail of the other. After a short chase the pursued slug turns back and contacts the right side of the pursuing slug. The slugs continue to entwine their foreparts so that their heads and necks are thus borne upwards above the rest of their bodies. Soon the entwisting foreparts bring the atrial pores into contact and coitus ensues as the penises are very rapidly entwisted together as they evert. ... At first the contiguous atrial pores appear much dilated, then swollen. Next a diskoid body with a screw-shaped keel appears. This is the penis which continues to evert while it entwines with the everting penis of the other slug. As initially everted, the organs appear more elongate than later. The period of engagement of the sex-organs is so very transient, a matter of seconds."

Webb found that the phallus flagellum is everted along with the phallus during mating, and suggested that it may aid in the retention of semen during phallus retraction.

The translucent yellow eggs, 2.0–2.2x1.8 mm in size, were found in soil and under planter trays in clutches of 10–60 during spring in an Auckland greenhouse.

L. valentiana can be a pest in gardens and greenhouses (e.g., Frömming 1954, Waldén 1961), but there have been no reports of plant damage in New Zealand to date.

Remarks. *L. valentiana* is polymorphic in body coloration and banding (e.g., Waldén 1961).

Owing to general similarities in body form and great variation in body pigmentation, dissection is needed to separate this species from *L. nyctelia*, which also occurs in New Zealand (see above). Also, because of close similarity in external appearance and somewhat similar phallus morphology, *L. valentiana* has often been confused with *L. marginata* (Müller, 1774).

An introduction to the literature on *L. valentiana* is provided by van Regteren Altena (1950), Quick (1960), Wiktor (1967, 1973, 1989), Bequaert & Miller (1973), Backhuys (1975), Likharev & Wiktor (1980), Castillejo (1982), Alonso *et al.* (1986).

Genus *Limacus* Lehmann

Limacus Lehmann, 1864: 145, type species *Limacus breckworthianus* Lehmann, 1864 = *Limax flavus* Linnaeus, 1758, by original designation.
Plepticolimax Malm, 1868: 62, type species *Limacus breckworthianus* Lehmann, 1864 = *Limax flavus* Linnaeus, 1758, by original designation.
Simrothia Clessin, 1884 (1884–85): 62, type species *Limacus breckworthianus* Lehmann, 1864 = *Limax flavus* Linnaeus, 1758, according to Wiktor (1983a).

Diagnosis. Phallus cylindrical, shorter than half of body length, with no internal folds starting from proximal phallus apex. Bursa copulatrix duct short, opening to oviduct. Vagina very short. Prostatic gland fused with oviduct in all but its very anterior part. Vas deferens almost half length of phallus. Phallus retractor well developed, inserted at phallus apex. Intestine with last loop very short, and with rectal caecum extending towards posterior of body cavity.

Haploid chromosome number 31.

Remarks. The number of species representing the genus *Limacus* is in dispute (Likharev & Wiktor 1980, Wiktor & Norris 1982, Wiktor 1983a, Evans 1978b, 1986, Forcart 1986, Wiktor 1994). A species of very similar external morphology, *Limax maculatus* Kaleniczenko, 1851, is known in Europe (Black Sea, Crimea, Caucasus, Turkey, probably Romania, Bulgaria). This species is also known by some of its junior synonyms (*L. grossui* Lupu, 1970 – Romania, Crimea; and *L. pseudoflavus* Evans, 1978 – British Isles). *L. flavus* has been introduced into various parts of the world, and has long been represented in New Zealand.

Limacus flavus (Linnaeus)

Figures 43, 47, 83, 124, 153, 179, 205, 249, C17, C18, M77–79; Map 17

flavus Linnaeus, 1758: 652 (*Limax*).
variegatus Draparnaud, 1801: 103 (in part) (*Limax*).
unguiculatus Brard, 1815: 115 (*Limacella*).
virescens d'Audebard de Férussac, 1819: 71 (*Limax*).
megalodontes Quoy & Gaimard, 1824: 428 (*Limax*).
antiquorum Sowerby, 1828 (1821–34): 158 (not of d'Audebard de Férussac, 1819) (*Limax*).
umbrosus Philippi, 1844: 102 (*Limax*).
canariensis d'Orbigny, 1839 (1836–42): 47 (*Limax*).
olivaceus Gould, 1852: 4 (*Limax*).
ehrenbergi Bourguignat, 1853: 3 (*Limax*).
deshayesi Bourguignat, 1861: 302 (*Limax*).
companyoi Bourguignat, 1863 (1863–70): 179 (*Limax*).
eubalius Bourguignat, 1864c: 35 (*Limax*).
breckworthianus Lehmann, 1864: 145 (*Limacus*).
bicolor Selenka, 1865: 105 (*Limax*).
baeticus Mabille, 1868: 145 (*Limax*).

Animal (Fig. 43a–c) up to 120 mm in body length. Mantle about 0.3 of body length. Dorsum rounded, with keel at hind end very short. Dorsum and mantle with an irregular network of dark grey-olive to greyish-green spots on paler whitish-yellow or orange-olive background; on sides dark pigment does not reach edge of foot. Sole pale yellow. Mucus yellow. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 47) thin, shiny white, oblong-oval, up to 13x8.8 mm. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Vestigial protoconch near posterior margin, not protruding, situated asymmetrically at left side. Organic sheet surrounding the shell, usually extending a short distance beyond calcified part; partially decalcified shells not uncommon.

Reproductive system, Fig. 83. Ovotestis rounded, completely embedded in lobes of digestive gland. Hermaphrodite duct short, mostly convoluted, ending in rounded talon partially embedded in linguiform albumen gland. Female part of spermoviduct posteriorly tubular, broadening anteriorly. Free oviduct moderately long, slender. Bursa copulatrix reservoir small, oval, on a short duct. Vagina very short. Prostatic gland very long and slender, not fused to oviduct at its very anterior end. Vas deferens short, opening just below phallus appendix, adjacent to phallus retractor muscle. Phallus cylindrical, 0.15–0.2 of body length, variously twisted and folded; internally proximal part with a series of longitudinal crenulate folds which, at the distal phallus, are followed by only 3 short but large folds of lobulate or crenulate margin. Atrium very short.

Phallus retractor short, arising from left margin of diaphragm below kidney in posterior of pallial complex.

Jaw (Fig. 124) 2.5 mm wide, marked transversely with fine striae which reticulate with finer striae following jaw contour.

Radula (Fig. M77–79) with 130–170 transverse rows of teeth, each varying around the formula 50–65+C+50–65. Ectocones and endocones of all teeth very poorly developed or absent. Central tooth on a broad basal plate; mesocone prominent, elongate. Transition from lateral to marginal teeth marked by basal plate becoming progressively smaller, and mesocone becoming progressively elongate and aculeate. Twentieth to 23rd tooth in each row most elongate, largest, then teeth becoming progessively smaller towards margin.

Digestive tract, Fig. 153. Buccal mass spheroidal. Oesophagus expanding to large crop, extending to about 0.7 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to about half length of crop, passing over anterior aorta branch, and producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor to form a further short posteriorly directed loop and running forwards to anus. Rectal caecum long, arising from last intestinal loop and extending along right side to reach posterior of body cavity.

Pallial complex (Fig. 179) located in posterior part of mantle. Kidney bean-shaped, its longest axis oblique to body axis, partially enclosing heart on its left side. Secondary ureter separating from left posterior part of kidney and describing an arc to right anterior part of pallial complex, where it inflates to form a urinary bladder. Heart in left anterior quarter of pallial complex, with ventricle directed posteriorly and to the right; aortic stem short. Lung heavily vascularised.

Free muscle system, Fig. 205. Cephalic retractor arising on dorsal body wall a little posterior to pallial complex and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising from left tentacular retractor branch near its origin from stem.

Central nervous system with cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia clearly closer to pedal ganglia than to cerebral ganglia. Visceral chain compact but with pleural, parietal, and visceral ganglia distinct; visceral ganglion to right of median plane.

Haploid chromosome number 31.

Type material. Described from Europe without precise type locality, but presumably from Sweden or England. The type material no longer exists.

Distribution. Because of the confusion of *Limacus flavus* with members of the genus *Limax* and its strong synanthropy, the original distribution is not known. Bruijns *et al*. (1959) considered *L. flavus* to be of Mediterranean origin. It occurs widely in western Europe, and has been introduced to many parts of the world, including Japan, China, St Helena, Madagascar, Canada, the U.S.A., South Africa, Australia, Rarotonga, Vanuatu, and New Zealand.

Recommended common name. Yellow cellar slug.

Material examined. New Zealand. AK. Te Atatu, 15 Sep 1974, R.A. & M.A. Cumber; 15 Feb 1978, M. Tocker, in shadehouse associated with potting plants. Glen Innes, 26 Jan 1978, L.M. Dean, in house cellar. Titirangi, 23 Nov 1969, P.S. Dale. **WO.** Hamilton, 27 Aug 1977, in stored firewood; 4 Sep 1977, under timber in garden; 10 Oct 1977, in pasture; 13 Nov 1977, under logs in park; 12 Jun 1978, in grassy area at roadside; 2 Aug

1978, on footpath at night; 24 Sep 1978, under logs in *Cupressus* shelter belt. Tokoroa, 26 Jun 1978, under *Pinus* logs; 8 Jan 1979, V.J. Crocker, under timber in garden. Waitomo, 19 Sep 1978, under limestone rocks in pasture. **BP**. Omokoroa, May 1997, P.C. Mayhill. **GB**. Gisborne, 11 Jan 1978, G. Halliwell. **TK**. Hawera, 6 Feb 1995, R. Harrison, abundant at night on moist carpet in shop. **WN**. Levin, 15 Nov 1992, A. Carpenter. Wellington, 29 Aug 1978, M. Peters, in stored firewood. **BR**. Greymouth, 16 Sep 1988, J.S. Paterson. **MC**. Halswell, Nov 1976, R.H. Blank. **DN**. Dunedin, 10 Jan 1978, D. Farrell. **SL**. Gore, 16 Jan 1978, A.J. McCraw.

Extralimital. Poland. Ostrów Wielkopolski, 2 May 1954, L. Berger, det. A. Wiktor. **South Africa**. Stellenbosch, Cape Province, 1978, coll. & det. W.F. Sirgel.

History in New Zealand. *L. flavus* was first recorded in New Zealand from Dunedin by Hutton (1879). A few years later Hutton (1883) added Greymouth as a locality. These records were quoted by Musson (1891), Suter (1891), and others without additional information. Taylor (1902–07(1902–21)) listed as localities Dunedin and Greymouth, after Hutton, plus Hokitika on the basis of specimens collected in 1905 by W.D. Roebuck. Suter (1913) considered the species both common and injurious to vegetables, but gave no further locality information. Thomson (1922) also regarded *L. flavus* as common, but gave only Dunedin, Greymouth, and Taranaki as localities. These records were repeated in subsequent literature without additional information (e.g., Whitten 1955, Powell 1979). While recognising the wide distribution of *L. flavus* in New Zealand, Barker (1979, 1982) noted that the extent of its dispersal was not fully documented.

Biology. *L. flavus* is a nocturnal, rather secretive animal. Despite its large size and being widespread in moist urban habitats, it is infrequently seen. It is not con-sidered an abundant species, and is poorly represented in New Zealand malacological collections.

In New Zealand *L. flavus* has been observed only in habitats closely associated with human dwellings, namely gardens, crevices of walls or wood stacks, on damp carpets and other floor coverings, and in cellars and outhouses. These are essentially the types of habitat most often occupied in Western Europe, although the species also occurs in woodland there (Quick 1960, Evans 1978b, 1986, Cook & Radford 1988). Kerney (1966) regarded *L. flavus* as a synanthropic species.

L. flavus feeds on decaying vegetable matter, fungi, and lichens (Taylor 1902–07 (1902–21), Frömming 1954, Cook & Radford 1988). It is an occasional pest in dwellings and commercial premises, making night forays to feed on moist, decaying carpet and associated microflora. Like *L. maximus*, this species exhibits marked homing behaviour, and several individuals tend to aggregate together at a single home site (Taylor 1902–07 (1902–21), Cook 1981, Chelazzi *et al.* 1988).

Individuals live for several years, and in Ireland Cook & Radford (1988) found them to be reproductive in their first autumn. Juveniles are most frequently encountered in New Zealand during winter to spring, reflecting the summer to early winter timing of egg laying. The eggs are commonly 6x4 mm but may be as large as 11 mm, translucent pale amber, and laid in chains of 20 or more. They hatch in 1–2 months at ambient temperatures, but are sensitive to low temperture (e.g., 5°C) (Cook & Radford 1988). The hatchlings are pale greenish yellow with characteristically blue ocular peduncles; the spotted pattern of the dorsal skin and mantle appears later in development.

L. flavus is capable of self-fertilisation (Evans 1983), but the frequency of this mode of reproduction, relative to mating and cross-fertilisation, is not known. In the present study mature slugs were observed to engage in trail following, without any apparent 'courtship' behaviour before mating (Fig. 254). The copulating slugs rapidly everted and spirally intertwined their phallic structures. Spermatozoa enclosed in a mucous mass were exchanged, and were transferred to the bursa copulatrix on withdrawal of the genitalia at the completion of copulation, which lasted less than 2 minutes. Further details on mating in this species are given by Gerhardt (1933).

Remarks. *L. flavus* of Europe has recently been recognised as comprising a species complex (Chatfield 1976, Evans 1978a, b, 1982, 1985, 1986, Likharev & Wiktor 1980, Wiktor & Norris 1982, Wiktor 1983a, Forcart 1986) (see above). All earlier information pertaining to *L. flavus* should therefore be viewed with caution.

L. flavus tends to be polymorphic in body coloration, and numerous variety names are to be found in the literature (e.g., Taylor 1902–07(1902–21), Hesse 1926, Quick 1960).

An introduction to the literature on *L. flavus* is provided by Germain (1930), Pilsbry (1948 (1939–48), van Regteren Altena (1950), Likharev & Rammel'meier (1952), Quick (1960), Giusti (1973, 1976), Wiktor (1973, 1983a, 1989), Backhuys (1975), Likharev & Wiktor (1980), Castillejo (1982), Alonso *et al.* (1986), and Evans (1986).

Genus *Limax* Linnaeus

Limax Linnaeus, 1758: 652, type species *Limax maximus* Linnaeus, 1758, designated by d'Audebard de Férussac (1819).

Krynickillus of authors. (Not *Krynickillus* of de Kaleniczenko, 1851, type species *Krynickillus melanocephalus* Kaleniczenko, 1851, by monotypy; Agriolimacidae.)

Parmacella of authors. (Not *Parmacella* of de Cuvier, 1804, type species *Parmacella olivieri* de Cuvier, 1804, by monotypy; Parmacellidae.)

Limacella Brard, 1815: 107, type species *Limacella parma* Brard, 1815 = *Limax maximus* Linnaeus, 1758, designated by Turton (1831). (Not of de Blainville, 1817, type species *Limacellus lactescens* de Blainville, 1817 = *Limax carolinianus* Bosc, 1802, by monotypy – synonym of *Philomycus* Rafinesque Schmalz, 1820; Philomycidae.)

Eulimax Moquin-Tandon, 1855: 22, type species *Limax maximus* Linnaeus, 1758, designated by Pilsbry (1922).

Diagnosis. Shell an asymmetrical, broadly oval internal plate with concentric growth lines radiating from vestigial protoconch at left posterior margin. Keel on body well developed but often very short. Pneumostome in right posterior part of mantle. Mantle shield with concentric ridges, their nucleus in mid-dorsal line. Jaw oxygnathic, with a median projection. Right ocular retractor passing forwards over phallus. Vagina absent; bursa copulatrix duct arising from distal phallus. Phallus long, with internal system of folds. Genital orifice immediately behind and below right ocular peduncle.

Remarks. About 90 species of *Limax* are recognised in 8 subgenera. Most are broadly Mediterranean, occurring from North Africa to eastern Europe and Asia Minor.

Subgenus *Limax*

Limax Linnaeus, 1758: 652, type species *Limax maximus* Linnaeus, 1758, by original designation.

Heynemannia Malm, 1868: 54, type species *Limax maximus* Linnaeus, 1758, designated by Wiktor (1983a).

Gestroa Pini, 1876: 83, type species *Limax maximus* Linnaeus, 1758, designated by Wiktor (1983a).

Chromolimax Pini, 1876: 87, type species *Limax cinereoniger* Wolf, 1803, designated by Wiktor (1983a).

Opilolimax Pini, 1876: 92, type species *Limax punctulatus* Sordelli, 1870, designated by Wiktor (1983a).

Stabilea Pini, 1876: 97, type species *Limax psarus* Bourguignat, 1862, designated by Wiktor (1983a).

Macroheynemannia Simroth, 1891: 303, type species *Limax maximus* Linnaeus, 1758, designated by Wiktor (1983a).

Diagnosis. Phallus long, cylindrical, with a retractor muscle. Bursa copulatrix reservoir small, on a short duct to distal phallus. Prostatic gland not fused with oviduct anteriorly. Vas deferens always well developed. Rectal caecum absent.

Haploid chromosome number 31.

Remarks. Subgenus *Limax* contains about 20 species, mostly native to the Mediterranean and Asia Minor. Represented in New Zealand by a single naturalised species.

Limax (*Limax*) *maximus* Linnaeus

Figures 44, 48, 84, 125, 154, 180, 206, 232, 250, C19, M80–82; Map 16

maximus Linnaeus, 1758: 652 (*Limax*).
cellarius Dezallier d'Argenville, 1757: 28 (*Limax*).
cinereus Müller, 1774: 5 (in part) (*Limax*).
parma Brard, 1815: 110 (*Limacella*).
antiquorum d'Audebard de Férussac, 1819: 68 (in part) (not *Limax antiquorum* d'Audebard de Férussac, 1819 = *Limax cinereoniger* Wolf, 1803) (*Limax*).
maculatus Nunneley, 1837: 46 (*Limax*).
sylvaticus Morelet, 1845: 33 (*Limax*).
vulgaris Moquin-Tandon, 1855: 28 (new name for *Limax cinereus* var. ß Müller, 1774, but as subsp.) (*Limax*).
mamelianus Bourgnignat, 1869: 4 (*Krynickillus*).
bocagei da Silva e Castro: 1873: 245 (*Limax*).

Slugs (Fig. 44a–f) up to 200 mm long, with specimens 100 mm long usually mature. Mantle about 0.3 of body length. Hind body distinctly keeled. Body yellowish white or grey; back usually with 6, 4, or 2 dark bands, these frequently interrupted to form a more or less spotted pattern; mantle irregularly spotted or marbled with dark pigment. Sole uniformly pale. Mucus clear. Locomotion by muscular pedal waves generated from posterior of sole. Genital orifice immediately posterior to right ocular peduncle.

Shell (Fig. 48) thin, shiny white, oblong-oval, up to 14 x6.7 mm. Dorsal surface weakly convex, with distinct growth lines. Ventral surface concave. Protoconch vestigial, non-protruding, situated asymmetrically at left side near posterior margin. An organic sheet surrounding shell, often remarkably broad.

Reproductive system, Fig. 84. Ovotestis elongate, reaching apex of body cavity or almost so, embedded in digestive gland. Hermaphrodite duct long, at first straight and slender, then wider and convoluted before narrowing to talon, which is deeply embedded in albumen gland. Female part of spermoviduct folded and voluminous. Free oviduct long and mostly slender, but dilated at entry into atrium. Bursa copulatrix reservoir small, oval, on a short duct opening to base of phallus, very close to atrium. Vagina absent. Prostatic gland fused to female oviduct

proximally, free anteriorly. Vas deferens thin, opening at apex of phallus adjacent to insertion of retractor muscle. Phallus cylindrical, its length half or more that of body, strongly convoluted, internally with a fold expanded proximally into a comb. Atrium short.

Phallus retractor short, arising from left margin of diaphragm in posterior part of pallial complex.

Jaw (Fig. 125) 3.5 mm wide, with a prominent medial projection and transversely scored with fine striae.

Radular ribbon (Fig. M80–82) comprising about 150 rows of teeth, each near the formula 20+50+C+50+20. Central tooth tricuspid, with a prominent mesocone flanked on either side by small, weak ectocones. First lateral tooth usually tricuspid, with prominent mesocone flanked by small endocone and ectocone. Lateral teeth with mesocone progessively more slender and elongate towards outer lateral field of radula; ectocone generally absent in 2nd or 3rd lateral tooth; endocone persisting to perhaps the 20th tooth. Marginal teeth markedly smaller than lateral teeth, with mesocone outer edge somewhat serrated.

Digestive tract, Fig. 154. Buccal mass spheroidal. Oesophagus quickly expanding to large crop, extending to about 0.6 of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta, then producing a short posterior loop overlying crop before again running forwards to pass over stem of cephalic retractor, and finally producing a long, posteriorly directed loop along right side of body cavity before running to anus.

Pallial complex (Fig. 180) located in posterior part of mantle. Kidney bean-shaped, its longest axis somewhat obliquely positioned relative to body axis, partially enclosing heart on its left side. Secondary ureter separating from left posterior part of kidney and describing an arc to right anterior quarter of pallial complex, where it inflates to form an elongate, tubular urinary bladder. Heart in left anterior quarter of pallial complex, with ventricle directed posteriorly and to the right; aortic stem short. Lung with a well developed vascular network.

Free muscle system, Fig. 206. Cephalic retractor attached on dorsal body wall a little posterior to pallial complex and passing forwards before dividing into left and right tentacle retractors; buccal retractor arising as a branch from stem or from left tentacle retractor; second anterior loop of intestine passing over cephalic retractor stem near its origin.

Central nervous system, Fig. 232. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia markedly closer to pedal ganglia than to cerebral ganglia. Visceral chain compact but with pleural, parietal, and visceral ganglia distinct; visceral ganglion to right of median plane.

Type material. Described by Linnaeus without precise type locality, but presumably from Sweden, as the *Fauna Suecica* is cited. The whereabouts of the type material is unknown; it is probably lost.

Distribution. Native to southern and western Europe and probably North Africa. Its original distribution is difficult to establish, since it has spread as a synanthrope to many areas, including Scandinavia, Russia, the Ukraine, and the Caucasus. It has also frequently been mistaken for *L. cinereoniger* Wolf, 1803 and other species in southern Europe (Wiktor 1983a). In addition to New Zealand, *L. maximus* has been introduced into Northern Europe, Canada, the U.S.A., Hawaii, Mexico, South America, and Australia.

Recommended common name. Tiger slug.

Material examined. New Zealand. ND. Kerikeri, 14 Jul 1977, B.J. Greaney. Otakairangi, 1 Nov 1978, in pasture. Whangarei, 5 Aug 1977, C.A. Sanders, associated with potted plants in nursery. **AK.** Otakinini, 20–21 Oct 1978, in pasture and under logs in *Cupressus macrocarpa* shelter belt. Te Atatu, Nov 1977, M. Tocker, associated with potting plants in nursery. Glen Eden, 20 Dec 1987 and 16 Feb 1978, M. Lessiter. Ranui, Aug 1974, C.H. Wearing. Mangere, 29 Oct 1975, N.A. Martin. **CL.** Whangamata, 25 Nov 1977, C.A. Scott, under logs. Waihi, 9 Aug 1978, E.H.A. Oliver. **WO.** Tahuna, 25 May 1976, under timber and stones in pasture. Ngatea, 7 Jan 1977, R.H. Blank, in pasture. Ohinewai, 18 Jul 1977, under timber in grassy road verge. Komakorau, 18 Jul 1977, in pasture. Tauwhare, 14 Dec 1994, under timber on ground. Matangi, Whewell's Bush, 14 Jan 1996, in *Podocarpus dacrydioides* forest remnant. Hamilton, 18 Oct 1976, on lawn at night; 20 Jan 1977, pairs mating on apple tree and house wall; 29 Jun 1978, in garden; 2 Aug 1978, in garden stone wall. Rukuhia, 24 May 1976, under logs at margin of peat lake; 20 Jul 1978, under logs in *Cupressus* shelter belt. Te Kowhai, Sep 1976, L.M. Newman, in stored firewood; 19 Sep 1978, in grassy area at roadside. Kaipaki, 17 Oct 1977, under *Eucalyptus* logs in pasture. Moanatuatua, 9 Oct 1977, in pasture and waste areas on recently drained peat bog. Ohaupo, 6 Jun 1984, under logs in shrubbery; 8 Nov 1992, under timber in garden. Horo Horo, 2 Jul 1977, under timber in picnic area. Waikeria, 11 Jan 1977, in pasture. Pirongia, 22 Mar 1977, in pasture. Tokoroa, 8 Jan 1979, V.J. Crocker, on footpath in early morning. Kinleith, 24 May 1980, R.M.G. McKenzie, on trunk of *Quercus.* **BP.** Opotiki, 12 Sep 1986, in dunes. Torere, 18 Nov 1977, under drift logs high up on gravel dune. Raukokore, 15 Sep 1992, under logs in disturbed coastal *Vitex lucens-Beilschmiedia tawaroa* forest. Whangaparaoa, 14 Sep 1992, under drift timber on dunes. **GB.** Te Araroa, 21 Sep 1992, under drift timber on dunes. Gisborne, 5 Apr 1977, N. Brown. **TO.** Wairakei, 11 May 1978, A. Zandvoort, under *Pinus* logs. **TK.** Hawera, 15 Jan 1979,

P.A. Powell, in garden. **WN**. Levin, 31 Mar 1993, A. Carpenter. Wellington, Newtown, 4 Sep 1988, A.T. Armstrong. **NN**. Motueka, 28 Nov 1979, P. Sutherland, in grape vines. Cable Bay, 25 Oct 1961, P.M. Johns, in coastal bush. Richmond, 30 Nov 1977, D. Nesbit. Aniseed Valley, 22 Jul 1978, C.C. Meikle, under *Pinus* logs in scrub; 18 Jan 1979, C.C. Meikle, under timber at roadside. **BR**. Greymouth, Aug 1977, under drift timber on dunes. Moana, 12 Mar 1990, P.C. Mayhill. Gladstone, 13 Mar 1990, P.C. Mayhill. **DN**. Flagstaff, 16 Feb 1994, under logs in *Pinus* plantation. Mosgiel, 15 Feb 1994, in leaf litter under *Pinus* hedge.

Extralimital. **England**. Sherborne, Gloucestershire, 14 Oct 1990. Queen Wood, Chiltern Hills, 16 Apr 1990. Bowsey Hill, Berkshire, 28 Apr 1990, in oak woodland. **Poland**. Wroclaw, 5 Jun 1965, M. Rydzewski, det. A. Wiktor.

History in New Zealand. The first record of *L. maximus* in New Zealand is that of Hutton (1879), who indicated that the species was present but rare in Dunedin. This record was repeated in subsequent literature (e.g., Hutton 1883, Musson 1891, Scharff 1891, Suter 1891, Crosse 1893, Taylor 1902–07(1902–21), Suter 1913, Quick 1952). Taylor (1902–07(1902–21)) added Wanganui as a locality on the basis of material collected in 1905. Longstaff (1912) recorded *L. maximus* as being found in Gisborne in 1910, while Thomson (1922) added Taranaki as a locality. Whitten (1955) listed the earlier Dunedin and Taranaki records, in addition to quoting A.W.B. Powell, who regarded the species as not uncommon in Auckland. Barker (1979, 1982) found *L. maximus* to be widespread in New Zealand.

Biology. *L. maximus*, the largest of the introduced slugs, is now widely dispersed throughout mainland New Zealand. It is most commonly found in association with buildings and gardens, although individuals will occasionally be found in pastures, exotic conifer plantations, *Leptospermum* scrub, and margins of native forests. In New Zealand *L. maximus* appears not to penetrate far into undisturbed forested areas, but can be abundant in modified forest remnants and secondary forest.

L. maximus is strictly nocturnal, hiding during the day beneath stones, fallen timber, deep leaf litter, and other damp places. It is not gregarious, and individuals return repeatedly to the same day-time resting site (Taylor 1902–07(1902–21), Pilsbry 1948(1939–48), Frömming 1954), apparently guided by olfactory cues (Gelperin 1974). It feeds primarily on decaying plant material and fungi (Barker & McGhie 1984, Cook & Radford 1988), but may damage to vegetable and horticultural crops (Barker & McGhie 1984). *L. maximus* feeds readily on kitchen refuse, and will make nightly forays to the compost bin. Perhaps because of its liking for soft-bodied carrion, and

its at times aggressive behaviour toward other slugs (Rollo & Wellington 1977, 1979), this species is often erroneously regarded as a predator.

The life cycle of *L. maximus* in New Zealand, described by Barker & McGhie (1984), closely follows that reported for the British Isles (Quick 1960) and North America (Sokolove & McCrone 1978). Growth occurs throughout the year and, given that individuals live for 3 or 4 years, there is always a wide range of body size in any given population. Mating occurs from February to May and is followed shortly by egg-laying. Greatest numbers of juvenile slugs occur from May to September. The maximum size attainable in New Zealand appears to be 95 mm resting (150 mm extended), whereafter gains are made in body weight but not in length. In dissected animals the genitalia become discernible in slugs over 40 mm in length, though there is little relationship between sexual maturity and body size.

Mating (Fig. 250) occurs at night. Preliminary courtship behaviour was observed to consist of circular crawling motions, with repeated body contact. After a period the slugs intertwine their bodies and become suspended by a stout mucus thread from an overhanging surface. While suspended with interwined bodies for 10–20 minutes, the pair evert their terminal genitalia and interwine their voluminous phalluses. Copious mucus production accompanies rotating motions of the phalluses, during which seminal material is apparently exchanged. Slow withdrawal of the genitalia occurs as the slugs re-ascend the mucus thread. The reader is referred to Adams (1898), Kew (1901), Gerhardt (1933, 1934), and van Regteren Altena (1960) for further information on the mating behaviour of this species.

The eggs, varying greatly in size about a mean of 5.0x 5.5 mm, are soft, translucent, and amber-coloured. They are laid in clusters of 20–100, and hatch in about 1 month in the field (approx. 14 days at 18–20°C: Prior 1983). The hatchlings are pale, translucent grey with a faint band visible on the mid dorsum and vinous ocular peduncles and inferior tentacles. Within 3 weeks the other body bands have appeared and begin breaking up, and the mantle becomes increasingly spotted or mottled.

Remarks. *L. maximus* is polymorphic in body coloration. Numerous variety names are to be found in the literature (e.g., Taylor 1902–07(1902–21), Hesse 1926, Quick 1960).

Entry into the extensive literature on *L. maximus* is provided by Germain (1930), Pilsbry (1948 (1939–48)), Likharev & Rammel'meier (1952), Quick (1960), Bequaert & Miller (1973), Wiktor (1973, 1983a, 1989), Backhuys (1975), and Likharev & Wiktor (1980).

Family MILACIDAE

Diagnosis. Herbivorous slugs up to 130 mm long, with internalised rudimentary shell. Body elongate, tapering posteriad, with a keel usually along back from posterior edge of mantle to end of body. Mantle anterior, covering less than 0.3 of body, with horseshoe-shaped groove opening posteriad; pneumostome in posterior right margin. Sole divided into 3 longitudinal zones, with chevron-shaped wrinkles on its surface. Suprapedal gland free in body cavity. Kidney elongate oval, aligned with body axis, partially enclosing heart on the right, with a large posterior lobe extending over rectum; secondary ureter separated from kidney, terminating without a bladder. Cephalic retractors arising from posterior edge of pallial complex. Right ocular retractor not passing over phallus. Buccal mass spheroidal. Jaw oxygnathic, with a medial projection. Radula with marginal teeth dagger-like or sword-like, sometimes with a small ectocone. Intestine with a single loop directed forwards. Genital orifice about one-third to one-half distance between right ocular peduncle and pneumostome. Genital organs with accessory glands, opening into vagina or atrium, and often with a prominent stimulator. Epiphallus a fleshy prolongation of phallus, producing elaborate spermatophores. Central nervous system with cerebropedal connectives equal in length and short. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 33 or 34.

Remarks. The taxonomic history and generic diagnostic characters of the Milacidae are provided by Wiktor (1981). The family comprises two genera (*Milax* Gray, 1855 and *Tandonia* Lessona & Pollonera, 1882), with about 50 species naturally distributed about the Mediterranean, the coasts of the Black Sea, and adjacent regions of southern and western Europe, Asia Minor, and northern Africa (Wiktor 1981, 1983a).

The Milacidae are represented in New Zealand only by naturalised species.

Genus *Milax* Gray

Limax of authors. (Not *Limax* of Linnaeus, 1758, type species *Limax maximus* Linnaeus, 1758, by original designation; Limacidae.)

Aspidoporus of authors. (Not *Aspidoporus* of Fitzinger, 1833, type species *Aspidoporus limax* Fitzinger, 1833, by monotypy – synonym of *Tandonia* Lessona & Pollona, 1882; Milacidae.)

Milax Gray, 1855: 174, type species *Limax gagates* Draparnaud, 1801, designated by Hesse (1926), also by Kennard & Woodward (1926) – ICZN Opinion 335 (1955a: 49, 57).

Amalia Moquin-Tandon, 1855: 19 (as a section of *Limax* Linnaeus, 1758), type species *Limax gagates* Draparnaud, 1801, designated by Wiktor (1981).

Lallemantia Mabille, 1868: 143, type species *Limax polyptyelus* Bourguignat, 1859 = *Limax gagates* Draparnaud, 1801, by monotypy.

Palizzolia Bourguignat, 1877: 15, type species *Palizzolia monterosati* Bourguignat, 1877, by monotypy.

Sansania Bourguignat, 1881: 11, type species *Limax larteti* Dupuy, 1870, by monotypy.

Pyrainea Lessona & Pollonera, 1882: 57, type species *Limax gagates* Draparnaud, 1801, by original designation.

Tandonia of authors. (Not *Tandonia* of Lessona & Pollonera, 1882, type species *Limax marginatus* Draparnaud, 1805 = *Limax rusticus* Millet, 1843 (not *Limax marginatus* Müller, 1774), designated by Hesse (1926); Milacidae.)

Cypria Simroth, 1910b: 158, type species *Amalia cypria* Simroth, 1906 = *Limax barypus* Bourguignat, 1866, by monotypy. (Not *Cypria* of Zenker, 1848; Ostracoda.)

Micromilax Hesse, 1926: 33, type species *Amalia cypria* Simroth, 1906 = *Limax barypus* Bourguignat, 1866, by original designation. New name for *Cypria* Simroth, 1910.

Diagnosis. Shell internal, a broadly oval arched plate with concentric lines of growth radiating from vestigial protoconch situated posteriad. Body keel very strongly arched. Genital accessory gland single, large, opening laterally to atrium. Atrium large, usually with one or more stimulators inside.

Haploid chromosome number 33 or 34.

Remarks. The priority of *Milax* Gray, 1855 over *Amalia* Moquin-Tandon, 1855 was established by Mörch (1865). The genus has been divided according to various systems (Simroth 1910a, Hesse 1926, Wagner 1930a, b), but Wiktor (1981) has shown that these are ill founded. Twelve *Milax* species are known, with a natural distribution from the Canary Islands through the Mediterranean and Black Sea regions to Transcaucasia. Several species have been distributed widely by man, and one has established in New Zealand.

Milax gagates (Draparnaud)

Figures 49, 52, 85, 103, 126, 155, 181, 207, 233, 251, C20, C21, M83–86; Map 18

gagates Draparnaud, 1801: 100 (*Limax*).

marginata of authors (not *Amalia marginata* Draparnaud, 1805 = *Limax rusticus* Millet, 1843).

maurus Quoy & Gaimard, 1824: 427 (*Limax*).

ascensionis Quoy & Gaimard, 1832: 145 (*Limax*).

carenata d'Orbigny, 1839 (1836–42): 47 (*Limax*).

carinata d'Orbigny, 1842 (1836–42): pl. 3 fig. 4–8 (not of Risso, 1826) (*Limax*).

fulginosus Gould, 1852: 5 (*Limax*).

antipodarum Gray, 1855: 177 (*Milax*).

plumbea Moquin-Tandon, 1855: 19 (as var. of *gagates* Draparnaud) (*Limax* (*Amalia*)).

polyptielus Bourguignat, 1859: 144 (new name for *Limax carenata* d'Orbigny) (*Limax*).

scaptobius Bourguignat, 1861 (1860–62): 43 (*Milax*).

pectinatus Selenka, 1865: 105 (*Limax*).

atratus Mabille, 1868: 144 (*Milax*).

hewstoni Cooper, 1872: 147 (*Limax* (*Amalia*)).

emarginatus Hutton, 1879: 331 (*Milax*).

tasmanicus Tate, 1881: 16 (*Milax*).

nigricolus Tate, 1881: 17 (*Milax*).

gaimardi Mabille, 1883: 51 (*Milax*).

verneaui Mabille, 1883: 51 (*Milax*).

raymondiana Simroth, 1888: 69 (as var. of *gagates* Draparnaud) (*Amalia*).

rava Williams, 1888: 89 (*Amalia*).

pallida Cockerell, 1891a: 340 (as var. of *antipodarum* Gray) (*Amalia*).

parryi Collinge, 1895a: 7 (*Amalia*).

babori Collinge, 1897b: 294 (*Amalia*).

santosi Torres Minguez, 1928: 117 (*Amalia*).

Crawling slugs (Fig. 49) up to 50 mm long. Mantle about 0.25 of body length. Body dark grey or blackish, rarely brown or orange-brown, paler towards foot margin, never spotted or banded; keel of similar coloration to body or darker. Sole uniformly pale grey, or with darker grey or blackish lateral zones and paler medial zone. Mucus clear.

Shell (Fig. 52) oval, white and shining, up to 5.5x2.8 mm. Dorsal surface concave, highest at posterior. Ventral surface flat. Vestigial protoconch located centrally or slightly to left in posterior part. Growth lines distinct. Irregular shells occur frequently owing to decalcification.

Reproductive system, Fig. 85. Ovotestis rather small, pale, lying amongst lobes of digestive gland. Hermaphrodite duct proximally slender and straight, distally distended, producing a small saccular talon at entry to large albumen gland. Female part of spermoviduct folded and voluminous. Free oviduct short, stout. Bursa copulatrix reservoir oval, on a stout duct. Vagina very short. Prostatic gland fused throughout its length to glandular part of female oviduct. Vas deferens very slender, terminating in apex of epiphallus. Epiphallus claviform, broad at proximal end, constricted on entry to phallus. Phallus irregular in shape, almost half as long as epiphallus, internally with a small conical papilla at entry of epiphallus. Atrium short. Accessory atrial glands clustered into a cream mass with about 20 short, coiled tubules connecting to atrial wall, carrying internally a stimulator. Atrial stimulator elongate, strongly flattened but for conical end, coiled, its inner surface smooth except for a few irregularly scattered, sharply pointed papillae near free end.

Spermatophore (Fig. 103) greatly elongate, with short branched processes covering one side, the other side smooth.

Phallus retractor slender, arising from diaphragm at medial left of pallial complex, inserted on epiphallus or at junction of epiphallus and phallus.

Jaw (Fig. 126) about 1.5 mm wide, with a rounded anteromedial projection.

Radular ribbon (Fig. M83–86) comprising about 90–100 rows of teeth, each with a formula varying around 28+17+C+17+28. Central tooth slightly smaller than laterals on either side, tricuspid, with a strong mesocone flanked by strong ectocones. Lateral teeth tricuspid, with a strong mesocone; endocone progessively reduced in size so as to be absent in early marginal teeth; ectocone similarly reducing in size but persisting in early marginal teeth. Marginal teeth elongate, mostly unicuspid, reducing in size towards radular margin.

Digestive tract, Fig. 155. Buccal mass spheroidal. Oesophagus quickly giving rise to a large crop extending to about 0.65 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta, then turning posterad to produce a loop which extends well beyond stomach with a rotation exceeding 360 degrees, finally running transversely forwards to anus.

Pallial complex (Fig. 181) occupying greater part of mantle. Kidney elongate bean-shaped, its longest axis approximately parallel to body axis, and with a large posterior lobe extending to the right under rectum and ureter. Secondary ureter separating from right posterior part of kidney and describing a short arc to its orifice at right mediolateral margin of pallial complex. Heart partially enclosed by kidney from right, its ventricle directed posteriorly and slightly to the left; aortic stem long, extending behind pallial complex before branching. Lung with a well developed vascular network.

Free muscle system, Fig. 207. Cephalic retractors arising from a single root at posterior end of pallial area but dividing immediately into 2 branches, the tentacular and buccal retractors, which themselves divide anteriorly into left and right branches. Right tentaclar retractor not crossing phallus to insert on ocular peduncle.

Central nervous system, Fig. 233. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain very compact, with all ganglia closely appressed; left parietal ganglion apparently fused with visceral ganglion, which lies to left of median plane.

Haploid chromosome number 33 or 34.

Type material. The whereabouts of Draparnaud's types is unknown; they are presumed lost. The type locality is France, presumably near Montpellier.

Distribution. *M. gagates* is often associated with modified habitats. It is native probably only to the Canary Islands and the coastal zone and islands of the western Mediterranean. It occurs in south-western Europe, and is certainly introduced to Germany, Finland, Japan, North and South America, Bermuda, Australia, New Zealand, and numerous islands of the Atlantic (e.g., St Helena) and Pacific (e.g., Juan Fernandez).

Recommended common name. Jet slug.

Material examined. New Zealand. Holotype *Amalia antipodarum* var. *pallida* Cockerell, [?locality], BMNH. **ND.** Whangarei Harbour, Horohoro Stack, R. Parrish, 12 Sep 1992. **AK.** Te Hana, 23 Feb 1994, in pasture. Otakinini, 20 Oct 1978, in pasture. Helensville, 21 Jun 1978, C. Mercer, in pasture. Mt Albert, 26 May 1976, N.A. Martin. Mt Wellington, 15 Aug 1977, R.M. Edwards. Titirangi, 4 Sep 1974, N.A. Martin. **CL.** Great Barrier I., Kawa, 16 Nov 1964, ?coll. (MONZ). Thames, 3 Mar 1976, in pasture. **WO.** Waikaretu, Dec 1977, P.C. Mayhill, under stones of limestone outcrop in pasture. Ngaruawahia, 8 Jul 1978, S. Armstrong. Whatawhata, 15 Dec 1993, C.W. Barker & G.M. Barker, in pasture. Hamilton, 7 Mar 1976, in pasture; 15 Jul 1977, in vegetable garden; 25 Oct 1977, 29 Apr 1978, 10 Jun 1978, 24 Sep 1978, and 2 Sep 1993, in pasture. Matangi, 6 Mar 1979, L.N. Robertson, in pasture. Matangi, 18 Jul 1980, R.N. Watson, in commercial asparagus. Ohaupo, 8 Nov 1992, in pasture; 8 Mar 1994, in garden. Hinuera, Dec 1992, in pasture. Raglan, 16 Jul 1977, in grassy area at roadside. Waikeria, 25 Aug 1980, in pasture. Waitomo, Sep 1975, in pasture. Oparure, 21 Sep 1978, in pasture. Mairoa, 9 Aug 1977, under limestone rocks in pasture. **BP.** Raukokore, 15 Sep 1992, in disturbed coastal *Vitex lucens-Beilschmiedia tawaroa* forest. **GB.** Waihirere, 21 Jun 1978, A.C. Firth, in pasture. Whangara Valley, 16 Nov 1977, in pasture; 14 Jun 1979, in maize stubble. **TK.** Normanby, 13 Dec 1977, W.J. Pengelly, in pasture. Hawera, 1 Dec 1977, W.J. Pengelly, in pasture. **HB.** Hastings, 18 Apr 1978, M. Stoodley, in pasture. **WI.** Whangaehu Valley, Mar 1977, G. Crouchley, in pasture. Bulls, May 1977, W. Stiefel, in pasture. **NN.** Rakopi, 17 Jan 1978, C.C. Meikle, in garden. Parapara Inlet, 30 Jul 1978, C.C. Meikle, in grassy area at roadside. **SC.** Timaru, undated, C. McLeod, in pasture. **DN.** Mosgiel, Aug 1982, T.G. Watson, in pasture. **Chatham Is.** Chatham I., Waitangi, 29 Sep 1976, in pasture. Pitt I., 30 Sep 1976, in pasture.

Extralimital. Australia. Scotsdale, Tasmania, Oct 1993, in pasture. **England.** Kenton, Devon, Apr 1989, in pasture. **Peru.** Cusco, 12 Feb 1981, R.P. Pottinger, in pasture. **South Africa.** Cape Town, Cape Province, 1978, W.F. Sirgel. Stellenbosch, Cape Province, 1978, W.F. Sirgel.

History in New Zealand. *M. gagates* has been known from New Zealand since material was collected in the Bay of Islands in 1840 as a result of the United States Exploring Expedition in the South Pacific. This material was described under the name *Limax fulginosus* Gould, 1852. On the basis of further New Zealand material, this species was subsequently described as new taxa, *Milax antipodarum* Gray, 1855 and *Milax emarginata* Hutton, 1879. The name *Milax gagates* was first applied to this species in New Zealand by Musson (1891).

Biology. *M. gagates* is widely distributed in the North and South islands, and occurs on the Chatham Islands. It is found in gardens and nurseries, field crops, pastures, and less commonly in greenhouses. It is often subterranean in habit, and has been associated with potato tuber and carrot root damage in both gardens and commercial plantings.

Mating (Fig. 251) has been observed on several occasions between animals held in capivity. In the initial stages, which generally occurred late in the evening, the slugs often circled clockwise, but movement was slow. Protrusion of the stimulator followed, and in some matings this was seen to be played briefly over the body of the partner. The pairing slugs assumed a near motionless state, with bodies closely appressed and curved. The stimulators became concealed by the close proximity of the slugs, and it appeared that each animal inserted the stimulator into the atrium of its partner. The termination of precopulatory courtship behaviour and the onset of copulation proper were difficult to distinguish as there was little external evidence of genital eversion and penetration.

The animals remained in a presumed copulatory state for 8–15 hours, during which there was little movement and little or nothing of their genitalia visible. As the animals separated, there was again little notable evidence of genital eversion, except that part of the received spermatophore was often seen protruding from the still partially dilated atrium. Full uptake of the spermatophore was achieved rapidly by movement in the atrium. Dissection of animals within 5 minutes of copulation revealed a spermatophore lodged in the bursa copulatrix of each slug.

These observations are generally consistent with those by Taylor (1902–07(1902–21)), Gerhardt (1936), and Wiktor (1987a, b), except that the reported period in copulation varies greatly. The prolonged copulatory period in this and other milacid species has generally been assumed necessary to effect spermatophore production and transfer. The presence of several spermatophores in the bursa copulatrix (Bett 1960) suggests that these slugs mate repeatedly during their breeding season. Karlin & Bacon (1960) reported *M. gagates* isolated from birth to be capable of self fertilisation and production of viable eggs.

Adults are most apparent in Waikato pastures in spring

and autumn, when mating pairs are occasionally discovered under shelter. Eggs and juveniles are most prevalent in late spring to summer and again in early winter, as are spent adults, which die on the soil surface several weeks after reproductive activity. This pattern of activity suggests a 6-month life cycle, similar to the breeding cycles of the related species *M. nigricans* (Philippi, 1836) under laboratory conditions (Quattrini 1970, Forcardi & Quattrini 1972).

The transparent eggs are relatively small at 2.0x1.5 mm to 2.8x1.8 mm. In clutches of 12–20, the eggs are usually deposited in chambers 30–50 mm deep, formed by the slugs borrowing into the soil. On occasion the eggs are deposited under cover on the soil surface.

Remarks. As discussed by Wiktor (1987b), several species – including *M. nigricans* (Philippi, 1836), *M. gasulli* Altena, 1974, and *M. ater* (Collinge, 1895) – closely resemble *M. gagates*. Examination of the papillation of the atrial stimulator and spination of the spermatophore is required for their separation. The validity of many identifications of *M. gagates* in earlier works consequently requires confirmation.

Limax fulginosus Gould, 1852, *Milax antipodarum* Gray, 1855 (= *M. antipoda* Pfeiffer of some authors), *M. emarginata* Hutton, 1879, and *Amalia antipodarum* var. *pallida* Cockerell, 1891 were all erected for specimens collected in New Zealand and thought to be native to this country. They are here placed in synonymy with *M. gagates*, as has been done previously (e.g., Suter 1913, Barker 1979).

I have examined, without dissection, the holotype of Cockerell's (1891a) var. *pallida* (in BMNH) and found it to be an immature *M. gagates*. Type material of *Limax fulginosus* is apparently lost (Dr C. Kessler, MCZH, pers. comm.), but Gould's (1852) description and figure fall within the range of variation of *M. gagates*. Type material corresponding to the species of Gray (1855) and Hutton (1879) could not be located.

Quick (1960) recognised a number of varieties in *M. gagates*, but several of these are now regarded as belonging to *M. nigricans*.

An introduction into the literature on *M. gagates* is provided by Germain (1930), Pilsbry (1948(1939–48)), van Regteren Altena (1950), Quick (1960), Backhuys (1975), Likharev & Wiktor (1980), Martin & Angulo (1986), and Wiktor (1987b).

Genus *Tandonia* Lessona & Pollonera

Limax of authors. (Not *Limax* of Linnaeus, 1758, type species *Limax maximus* Linnaeus, 1758, by original designation; Limacidae.)

Amalia of authors. (Not *Amalia* of Moquin-Tandon, 1855, type species *Limax gagates* Draparnaud, 1801, designated by Wiktor (1981) – synonym of *Milax* Gray, 1855; Milacidae.)

Milax of authors. (Not *Milax* of Gray, 1855, type species *Limax gagates* Draparnaud, 1801, designated by Hesse (1926); Milacidae.)

Tandonia Lessona & Pollonera, 1882: 54, type species *Limax marginatus* Draparnaud, 1805 = *Limax rusticus* Millet, 1843 (not *Limax marginatus* Müller, 1774; Limacidae), designated by Hesse (1926).

Subamalia Pollonera, 1887a: 5, type species *Amalia robici* Simroth, 1885, designated by Hesse (1926).

Macrothylacus Wagner, 1930a: 46 (as a subgenus of *Milax* Gray), type species *Milax jablanacensis* Wagner, 1930, by original designation and monotypy.

Promilax Wagner, 1930a: 50 (as a section of *Milax* Gray), type species *Amalia baldensis* Simroth, 1910, designated by Wiktor (1981).

Diagnosis. Shell internal, a broadly oval arched plate with concentric lines of growth radiating from vestigial protoconch situated posteriad. Body keel variously arched. Jaw oxygnathic, with a median projection. Genital accessory glands 2 or more in number, opening laterally to vagina below insertion of spermathecal duct. Atrium small, without a stimulator inside.

Haploid chromosome number 33 or 34.

Remarks. About 36 species of *Tandonia* are known, most from the Balkan Peninsula. Several have been widely dispersed through the activities of man. The genus is represented in New Zealand by two naturalised species.

Tandonia budapestensis (Hazay)

Figures 50, 53, 86, 104, 127, 156, 182, 208, 234, 252, C22, M87–90; Map 19

gagates Menegazzi, 1855: 64 (not of Draparnaud, 1801) (*Limax*).

gracilis Leydig, 1876: 276 (not of Rafinesque Schmaltz, 1820) (*Limax*).

budapestensis Hazay, 1881: 37 (*Amalia*).

cibiniensis von Kimakowicz, 1884: 103 (*Amalia*).

valachicus Grossu & Lupu, 1961: 133 (as a subsp. of *gracilis* Leydig) (*Milax*).

Slender, crawling slugs (Fig. 50) up to 70 mm long. Mantle about 0.25 of body length. Keel weakly arched. Body blackish to dark brown in appearance owing to dense, dark speckling on a dull cream or orange background, never

spotted or banded; keel olive or dull orange without dark speckling; pneumostome with an inconspicuous pale grey border. Sole dull orange, ashen, or blackish, often darker along margins. Mucus very thick, viscous, transparent orange or yellow.

Shell (Fig. 53) oval, brownish, up to 3.6x2.4 mm. Dorsal surface concave, highest at posterior. Ventral surface flat to concave. Vestigial protoconch located centrally and protruding in posterior part. Growth lines distinct.

Reproductive system, Fig. 86. Ovotestis large, consisting of numerous follicles forming an elongate cluster, spirally twisted amongst lobes of digestive gland. Hermaphrodite duct long, proximally slender and straight, distally distended and convoluted, producing a small saccular talon at entry to modest albumen gland. Spermoviduct folded and voluminous, with a well developed prostatic gland running throughout its length. Free oviduct short, slender. Bursa copulatrix reservoir oval, sometimes clearly narrowed at apex, on a stout duct. Vagina very short. Vas deferens very slender, long, terminating asymmetrically in apex of epiphallus. Epiphallus cylindrical or claviform, broad at proximal end, constricted on entry to phallus. Phallus irregular in shape but somewhat rounded, approximately as long as epiphallus, internally with a small conical papilla at entry of epiphallus. Atrium short, tubular, with internal surface minutely papillate but lacking a stimulator. Accessory glands 2 in number, closely adhering to vagina and connected to it by several thin tubules.

Spermatophore (Fig. 104) slender, about 16 mm long, its exterior surface covered with short, branched processes.

Phallus retractor well developed, arising from diaphragm at left posterior of pallial complex, inserted on epiphallus or at junction of epiphallus and phallus.

Jaw (Fig. 127) about 1.5 mm wide, with a rounded anteromedial projection.

Radular ribbon (Fig. M87–90) comprising about 90–110 rows of teeth, each with a formula varying around 40+7+C+7+40. Central tooth slightly smaller than lateral teeth on either side, tricuspid, with a strong mesocone flanked by strong ectocones. Lateral teeth tricuspid, with a strong mesocone; endocone progessively reducing in size so as to be absent in early marginal teeth; ectocone similarly reducing in size but persisting in early marginal teeth. Marginal teeth mostly unicuspid, elongate and slender, reducing in size towards radular margin.

Digestive tract, Fig. 156. Buccal mass spheroidal. Oesophagus quickly giving rise to a large crop extending to about 0.65 length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, running directly forwards to pass over anterior aorta, then producing a posterior loop which extends well beyond stomach, and finally running forwards to anus.

Pallial complex (Fig. 182) located under posterior part of mantle. Kidney oval, its longest axis approximately parallel to body axis, and with a large posterior lobe extending to the right under rectum and ureter. Secondary ureter separating from right posterior part of kidney and running directly to orifice at right mediolateral margin of pallial complex. Heart partially enclosed by kidney from right, its ventricle directed posteriorly and slightly to the left; aortic stem long, extending behind pallial complex before branching. Lung with a moderately developed vascular network.

Free muscle system, Fig. 208. Cephalic retractors arising from a single root at posterior end of pallial area, but soon dividing into 2 branches, the tentacular and buccal retractors, which themselves divide anteriorly into left and right branches. Right ocular retractor not passing over phallus to insert on ocular peduncle.

Central nervous system, Fig. 234. Cerebral ganglia united by a very short and indistinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact; right parietal and pleural ganglia closely appressed; left parietal and pleural ganglia fused; visceral ganglion to right of median plane.

Haploid chromosome number 33.

Type material. Leydig's type material was collected from the environs of Tubingen, Germany.

Distribution. The original range of *T. budapestensis* has not been ascertained. It probably occurred in the southern Alps and the northern Balkans of Europe, and spread as a synanthrope (Wiktor 1987b). It is now known from Austria, Italy, Germany, Switzerland, Hungary, Romania and – clearly as an introduction – from Turkey, Bulgaria, Yugoslavia, Czechoslovakia, Poland, Belgium, Netherlands, Great Britain, and New Zealand.

Recommended common name. Budapest slug.

Material examined. New Zealand. ND. Kerikeri, 14 Dec 1978, B.J. Greaney, in garden. AK. Mt Wellington, 15 Aug 1977, R.M. Edwards, associated with potted plants in nursery. Ellerslie, 15 Aug 1977, R.M. Edwards, in nursery; 18 Oct 1977, J.C. Curd & R.M. Edwards, in nursery. Te Atatu, 16 Aug 1975, M.A. Cumber. Mt Albert, 27 May 1976, N.A. Martin. Titirangi, 18 Sep 1974 and 14 Dec 1976, N.A. Martin. WO. Hamilton, 12 Sep 1976, 7 Jan 1977, 13 Jul 1977, 29 Jun 1978, and 21 Sep 1978, in gardens. Waitomo, 22 Jun 1976 and 19 Sep 1978, under limestone rocks in pasture.
Extralimital. England. Sherborne, Gloucestershire, 14 Oct

1990. Maidenhead Thicket, Berkshire, 28 Apr 1990. **Ireland**. Killarney, Kerry, 24 Aug 1990, under stones in garden. Ballyvary, Mayo, 27 Aug 1990, in rock wall. **Romania**. Bucharest, Oct 1964, D. Lupu, in park. **Scotland**. Auchincruive, Dumfries & Galloway, 12 Sep 1990, in garden.

History in New Zealand. First recorded in New Zealand by Barker (1979), at a time when it was apparently restricted to the northern North Island (Northland, Auckland, Waikato).

Biology. *T. budapestensis* occurs in New Zealand in gardens, nurseries, greenhouses, and less commonly in pastures. It is known in Europe as a pest of root crops such as potatoes, and instances of this type of damage have been recorded in New Zealand.

Mating behaviour (Fig. 257) has not been observed in New Zealand. Pairs in copulation have been collected in spring, and frequently had spermatophores in the bursa copulatrix. In Britain mating of *T. budapestensis* occurs from November to January (Quick 1960), while in Czechoslovakia mating has been observed from April to September (Hudec 1963). According to Quick (1960), courtship and copulation is prolonged, usually beginning at night and extending to the afternoon of the following day, or even longer. During copulation the atria, phalluses, and accessory glands are everted.

The yellow, leathery eggs, 3.0x2.25 mm, are laid in clutches of 8–15 in the soil. Juvenile slugs have been collected during spring and summer.

Remarks. Phillips & Watson (1930), Quick (1960), Wiktor (1973, 1983a, 1987b, 1989), and Likharev & Wiktor (1980) provide entry into the literature on *T. budapestensis*.

Tandonia sowerbyi (d'Audebard de Férussac)

Figures 51, 54, 87, 105, 128, 157, 183, 209, 235, C23, M91–94; Map 20

marginatus of authors (not of Müller, 1774; not of Draparnaud, 1805).
sowerbii d'Audebard de Férussac, 1823 *in* d'Audebard de Férussac & Deshayes 1820–51: 96 (*Limax*) (invalid original spelling for *sowerbyi* – ICZN Opinion 336, 1955b: 87).
carinatus Risso, 1826: 56 (*Limax*).
argillaceus Gassies, 1856: 232 (*Limax*).
etruscus Issel, 1868: 69 (*Limax*).
barbarus Mabille, 1869: 60 (*Milax*).
fulva Paulucci, 1879: 22 (as var. of *Limax marginatus* Draparnaud; not of Müller, 1774) (*Amalia*).
mongianensis Paulucci, 1879: 23 (as var. of *Limax marginatus* Draparnaud; not of Müller, 1774) (*Amalia*).

hessei Boettger, 1882: 96 (*Amalia*).
kobelti Hesse, 1882: 95 (*Amalia*).
tyrrena Lessona & Pollonera, 1882: 56 (*Amalia*).
benoiti Lessona & Pollonera, 1882: 105 (as var. of *Limax gagates* Draparnaud) (*Amalia*).
pallidula Cockerell, 1890: 286 (as subsp. of *carinatus* Risso) (*Amalia*).
maculata Collinge, 1895b: 336 (not of Koch & Heynemann, 1874) (*Amalia*).
pratensis Torrez Minguez, 1923: 6 (*Amalia*).
collingei Hesse, 1926: 139 (*Milax*) (new name for *Amalia maculata* Collinge, 1895).

Crawling slugs (Fig. 51) up to 70 mm long. Mantle about 0.25 of body length. Keel very strongly arched. Coloration rather variable, with body and mantle usually brownish yellow in appearance owing to diffuse blackish pigment forming irregular reticulation, never spotted or banded; keel yellow or orange, without dark speckling; pneumostome with a pale border. Sole creamy, with orange along margins. Mucus very thick, viscous, transparent orange or yellow.

Shell (Fig. 54) evenly oval, white, up to 5.6x2.8 mm. Dorsal surface concave, highest at posterior. Ventral surface flat or convex. Vestigial protoconch located centrally in posterior part. Growth lines distinct.

Reproductive system, Fig. 87. Ovotestis large, consisting of numerous follicles forming an elongate cluster, spirally twisted amongst lobes of digestive gland. Hermaphrodite duct long, proximally slender and straight, distally distended and convoluted, producing a small saccular talon at entry to modest albumen gland. Spermoviduct folded and voluminous, with well developed prostatic gland running throughout its length. Free oviduct moderately long, slender. Bursa copulatrix reservoir elongate with a narrow apical prolongation, on a short, slender duct. Vagina very short. Vas deferens very slender, long, terminating asymmetrically, almost laterally, in apex of epiphallus. Epiphallus elongate conical, broadening from a small apical knob at proximal end, its insertion on phallus marked by a sharp constriction. Phallus irregular cylindrical, approximately 0.3–0.5 of length of epiphallus, internally with a small, conical papilla at entry of epiphallus. Atrium short, bulbous, internally with fine folds and plate-like thickening, but lacking a stimulator. Accessory glands comprising numerous finger-like tubules and ducts surrounding vagina at entry to atrium.

Spermatophore (Fig. 105) elongate, at first very slender and surrounded by fan-like membranous processes in 4 rows before broadening to a smooth medial section, then covered with small branched processes before narrowing slightly to rounded tip.

Principal phallus retractor well developed but rather

short, arising from diaphragm at left posterior of pallial complex near origin of cephalic retractors, inserted on epiphallus. A pair of short supplementary muscles arising from body wall and inserted at distal end of epiphallus.

Jaw (Fig. 128) about 1.5 mm wide, with a rounded anterior medial projection.

Radular ribbon (Fig. M91–94) comprising about 110–120 rows of teeth, each with a formula varying around 35+12+C+12+35. Central tooth slightly smaller than lateral teeth on either side, tricuspid, with a strong mesocone flanked by strong ectocones. Lateral teeth tricuspid, with a strong mesocone; endocone progressively reducing in size so as to be absent in early marginal teeth; ectocone similarly reducing in size but persisting in early marginal teeth. Marginal teeth mostly unicuspid, elongate, reducing in size towards radular margin.

Digestive tract, Fig. 157. Buccal mass spheroidal. Oesophagus quickly giving rise to a large crop extending about 0.7x length of body cavity. Stomach a simple curvature, with 2 ducts to digestive gland. Intestine arising from left lateral aspect of stomach, rotating 270 degrees around crop to run forwards over anterior aorta, then producing a posterior loop which extends well beyond stomach, and finally running forwards to anus making a further rotation of 360 degrees.

Pallial complex (Fig. 183) occupying posterior part of mantle. Kidney oval, its longest axis approximately parallel to body axis, with a large posterior lobe extending to right under rectum and ureter. Secondary ureter separating from right posterior part of kidney and running directly to its orifice at right mediolateral margin of pallial complex. Heart partially enclosed by kidney from right, its ventricle directed posteriorly and slightly to the left; aortic stem long, extending behind pallial complex before branching. Lung with a moderately developed vascular network.

Free muscle system, Fig. 209. Cephalic retractors arising from a single root at posterior end of pallial area, but immediately dividing into 2 branches, the tentacular and buccal retractors, which themselves divide into left and right branches. Right ocular retractor not crossing over phallus to insert on ocular peduncle.

Central nervous system (Fig. 235) with cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives short, their length less than width of cerebral ganglia. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain very compact; left parietal ganglion fused with visceral ganglion, which is slightly to the left of median plane.

Haploid chromosome number 34.

Type material. The types, collected from the vicinity of London, England, are presumed lost (ICZN Opinion 336, 1955b: 107).

Distribution. The original range has been difficult to establish because *T. sowerbyi* tends to be highly synanthropic. It now occurs in coastal Mediterranean and southwest European areas, and has been introduced into South America and New Zealand.

Recommended common name. Sowerby's slug.

Material examined. New Zealand. **AK**. Otakinini, 20–21 Oct 1978, in pasture. Te Atatu, 16 Aug 1974, M.A. Cumber. Mt Albert, 27 May 1976, N.A. Martin. Mt Wellington, 15 Aug 1977, R.M. Edwards, in nursery. Ellerslie, 15 Aug 1977, R.M. Edwards, in nursery. **WO**. Matangi, 20 Oct 1975 and 8 Nov 1976, N.A. Martin, in pasture. Hamilton, 15 Oct 1977, 24 Oct 1977, 28 Nov 1977, and 24 Sep 1978, in gardens; 16 Oct 1993, in pasture. **GB**. 3 Nov 1978, N. Harding, in pasture. **TK**. Normanby, 13 Dec 1977, W.J. Pengelly, in pasture. **HB**. Napier, 1 Nov 1978, R.F. Lowe. **WI**. Bulls, May 1977, W. Stiefel, in pasture. **MC**. Christchurch, Nov 1976, R.H. Blank. **SC**. Timaru, C. McLeod, in pasture.

Extralimital. **England**. Chippenham, Wiltshire, 16 Jun 1990, in rock wall. Hurley, Berkshire, 3 May 1990, in pasture. **Ireland**. Killarney, Kerry, 24 Aug 1990, in grassy area at roadside.

History in New Zealand. Quick (1960) suggested that *T. sowerbyi* may occur in New Zealand. This was confirmed by Barker (1979), who found it to be widely distributed in both North and South islands.

Biology. In Europe *T. sowerbyi* occurs mainly in open habitats such as grasslands, arable fields, and gardens, sheltering under stones and pieces of wood. In New Zealand it has been collected principally from pasture. It burrows actively in soil and, on the basis of European experience, has the potential to inflict considerable damage on root crops such as potatoes and carrots.

Little is known of the life cycle of *T. sowerbyi*. In Europe mating occurs in autumn (Quick 1960, Wiktor 1987b). According to Quick (1960), after a courtship involving trail following and circling the pair copulate and remain united for 12–18 hours. Taylor (1902–07(1902–21)) noted the occurrence of more than one spermatophore in the bursa copulatrix, indicating that multiple matings sometimes occur. The pliable eggs, 4x3.5 mm to 5x4 mm and translucent pale amber, are laid in the soil in clusters of about 12. Hatchlings are 8 mm long, with a conspicuous pale keel. The mantle is speckled with black and sometimes has a dark median streak, which may be retained into adulthood.

Remarks. *T. sowerbyi* is easily distinguished from other *Tandonia* species by the characteristics of the bursa copulatrix, phallus, and epiphallus. In the literature it may have been confused with *T. rustica* (Millet, 1843).

Quick (1960) recognised several varieties of *T. sowerbyi* based on variation in body coloration.

An introduction into the literature on *T. sowerbyi* is provided by Germain (1930), Quick (1960), Giusti (1976), Wiktor (1983a, 1987b), and Martin & Angulo (1986).

Family PUPILLIDAE

Diagnosis. Herbivorous holopod snails, oviparous or ovoviviparous. Shell small, cylindriform to conical, frequently with apertural teeth; capable of fully housing the animal. Sole uniform, without a caudal mucus gland. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw aulacognathic. Radula with marginal teeth bearing numerous cusps, on broad, short basal plates. Intestine with a single loop directed forwards. Kidney very long, divided internally into 2 distinct regions, the anterior region functioning as a primary ureter, but without a secondary ureter. Columellar muscle branching at or a short distance from its origin into left and right cephalic retractor bundles; buccal retractor associated with left branch, tail fan associated with right branch. Right ocular retractor crossing phallus. Genital orifice immediately behind and below right ocular peduncle, or more posteriad, midway between right ocular peduncle and pneumostome. Spermoviduct formed; prostatic gland short, confined to proximal pallial gonoduct in ovoviviparous forms; prostatic gland longer in oviparous forms. Bursa copulatrix duct varying from long to short, with or without a diverticulum. Epiphallus present, often with a flagellum. Phallus frequently with an apical caecum and always with well developed appendix and gland. Phallus retractor arising from diaphragm, bifurcating to insert on phallus and phallial appendix. Central nervous system with cerebropedal connectives subequal in length and relatively long. Pleural ganglia closer to cerebral ganglia than to pedal ganglia. Visceral ganglion chain moderately concentrated.

Chromosome number unknown.

Remarks. The phylogeny of pupilloid snails has not been fully resolved, and the limits of the family Pupillidae have often been disputed. The family name is used here in its restricted sense for Pupillinae + Lauriinae + Argninae.

The family is represented by numerous species in the genera *Lauria* Gray, 1840, *Leiostyla* Lowe, 1852, *Enneopupa* Boettger, 1889, *Agardhia* Gude, 1911, and *Euxinolauria* Lindholm, 1924.

Subfamily LAURIINAE

Diagnosis. Epiphallus lacking a flagellum. Phallus frequently with an apical caecum.

Genus *Lauria* Gray

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Turbo of authors. (Not *Turbo* of Linnaeus, 1758, type species *Turbo marmoratus* Linnaeus, 1758, designated by de Montfort (1810); Turbinidae.)

Bulimus of authors. (Not *Bulimus* of Scopoli, 1786 (1786–88), type species *Bulimus haemastomus* Linnaeus, 1758, designated by Gray (1847) – synonym of *Megalobulimus* Miller, 1878; Acavidae.)

Pupa of authors. (Not *Pupa* of Röding, 1798, type species *Pupa grisebia* Röding, 1798 = *Voluta solidula* Linnaeus, 1758, designated by Suter (1913) – synonym of *Solidula* Linnaeus, 1758; Acteonidae. Not *Pupa* of de Monet de Lamarck, 1801, type species *Turbo uva* Linnaeus, 1758, by monotypy – synonym of *Cerion* Röding, 1798; Cerionidae. Not *Pupa* of Draparnaud, 1801, type species *Pupa secale* Draparnaud, 1801, by monotypy [ICZN Opinion 335, 1955a: 47] – synonym of *Abida* Turton, 1831; Chondrinidae.)

Clausilia of authors. (Not *Clausilia* of Draparnaud, 1805, type species *Turbo bidens* Montagu, 1803 = *Turbo bidentatus* Ström, 1765, designated by Turton (1831) [ICZN Opinion 119, 1931: 23; Opinion 335, 1955a: 56]; Clausiliidae.)

Odostomia of authors. (Not *Odostomia* of Fleming, 1813, type species *Turbo plicatus* Montagu, 1803, designated by Gray (1847); Pyramidellidae.)

Cochlodonta d'Audebard de Férussac, 1821: 63 (as a subgenus of *Helix* Linnaeus), type species *Pupa umbilicata* Draparnaud, 1801 = *Turbo cylindracea* da Costa, 1778, designated by Pilsbry (1922–26).

Pupilla of authors. (Not *Pupilla* of Fleming, 1828 (1827–28), type species *Pupa marginata* Draparnaud, 1801 = *Turbo muscorum* Linnaeus, 1758, by monotypy [ICZN Opinion 335, 1955a: 49, 58]; Pupillidae.)

Cochlodon Lowe, 1831: 62 (as a subgenus of *Helix* Linnaeus), type species *Helix (Cochlodon) anconostoma* Lowe, 1831 = *Turbo cylindracea* da Costa, 1778, designated by Pilsbry (1922–26) (emendation of *Cochlodonta* d'Audebard de Férussac, 1821).

Lauria Gray, 1840: 193 (as subgenus of *Pupa* Draparnaud), type species *Pupa umbilicata* Draparnaud, 1801 = *Turbo cylindracea* da Costa, 1778, designated by Herrmannsen (1847) [ICZN Opinion 335, 1955a: 49, 57].

Eruca Swainson, 1840: 334 (as subgenus of *Clausilia* Drap-
arnaud), type species *Pupa umbilicata* Draparnaud, 1801 =
Turbo cylindracea da Costa, 1778, designated by Herr-
mannsen (1847).

Stomodonta of authors. (Not *Stomodonta* of Mermet, 1843,
listed in synonymy of *Abida* Turton, 1831, Chondrinidae, by
Zilch (1959–60), type designation not traced.)

Gastrodon Lowe, 1852: 275 (as subgenus of *Pupa* Draparnaud,
1801), type species *Pupa fanalensis* Lowe, 1852 = *Turbo
cylindracea* da Costa, 1778, by monotypy. (Not *Gastrodon*
of Rafinesque Schmaltz, 1815; Pisces.)

Charadrobia of authors. (Not *Charadrobia* of Albers, 1854, type
species *Helix cheilogona* Lowe, 1831, designated by von
Martens (1860) – synonym of *Leiostyla* Lowe, 1852; Pupil-
lidae.)

Reinhardtia Boettger, 1879: 29 (as section of *Pupa* Drap-
arnaud), type species *Turbo cylindracea* da Costa, 1778,
designated by Pilsbry (1922–26).

Diagnosis. Shell small, perforate, ovate to cylindriform,
with usually a deeply penetrating angular lamella, some-
times with other aperture barriers but always lacking
parietal lamellae in adults. Juvenile stages with lamellae
on parietal wall and short radial plicae at various intervals
within basal margin. Animal with ocular peduncles and
inferior tentacles.

Remarks. All recent authors assign to *Lauria* Gray, 1840
only species with reduced aperture armature; they assign
the fully toothed forms to genus *Leiostyla* Lowe, 1852.
Zilch (1959–60, p. 171) writes that adult *Lauria* have one
parietal, one columellar, and one angular lamella. As poin-
ted out by Manganelli *et al.* (1990), *Lauria* s.s. never have
any parietal lamellae. *Pupa fasciolata* Morelet, 1860,
which sometimes has a reduced parietal lamella, is the type
species of *Senilauria* Pilsbry, 1934 (new name for *Pet-
rarca* Pilsbry, 1922), regarded as a subgenus of *Lauria*
by Zilch (1959–60, 1985) and Backhuys (1975). Pilsbry
(1922–26) has underlined that *P. fasciolata* could be a
"degenerated" *Leiostyla*. This opinion was accepted by
Manganelli *et al.* (1990), who transferred this species to
Leiostyla. They comment that other species currently
placed in *Lauria* might be *Leiostyla* with a reduced aper-
tural armature. Thus, the diagnoses for subfamily Laurinae
and its species-group taxa are likely to be subject to change
as further species are studied anatomically. The placement
of *Senilauria* in *Leiostyla* leaves no formal subgeneric div-
ision of *Lauria*.

Lauria species are distributed in Western Europe, Med-
iterranean, eastern Atlantic islands, and Africa to the sub-
saharan zone. One successful species, *L. cylindracea* (da
Costa, 1778) dominates the entire genus by its compara-
tively very large natural distribution, which largely coin-
cides with that of the genus.

Almost all taxa placed in *Lauria* s.s. have similar shells.
Given this, and the fact that the anatomy for most is un-
known, the systematic relationships and species limits of
nominal *Lauria* remain uncertain.

Lauria cylindracea (da Costa)

Figures 55, 88, 129, 158, 184, 210, 236, C24, M19–22,
M95, M96; Map 21

muscorum of authors (not of Linnaeus, 1758).
cylindraceus da Costa, 1778: 89 & errata (*Turbo*).
umbilicata Draparnaud, 1801: 58 (*Pupa*).
unidentatus Vallot, 1801: 6 (*Bulimus*).
drapernaudii Leach, 1831: 98 (*Pupilla*).
anconostoma Lowe, 1831: 62 (*Helix* (*Cochlodon*)).
helenica Benson, 1851: 263 (*Pupa*).
fanalensis Lowe, 1852: 275 (*Pupa* (*Gastrodon*)).
grevillei Chitty, 1853: 17 (*Pupa*).
helenensis Pfeiffer, 1856: 207 (*Pupa*).
bocconiana Benoit, 1857: 144 (*Helix*).
anconostoma var. *cristula* Mousson, 1858: 167 (*Pupa*).
poupillieri Bourguignat, 1864b: 89 (*Pupa*).
milleri Dohrn, 1869: 11 (not of Pfeiffer) (*Pupa*).
debilis Mousson, 1872: 124 (*Pupa*).
?bruguierei Jickeli, 1875: 112 (*Pupa*).
dohrni Pfeiffer, 1877: 371 (new name for *milleri* Dohrn) (*Pupa*).
perdubia Wollaston, 1878: 513 (as var. of *dohrni* Pfeiffer)
(*Pupa*).
misella Paulucci, 1882–83: 279 (as var. of *cylindraceus* da
Costa) (*Pupa*).
tabularis Melvill & Ponsonby, 1893: 20 (*Pupa*).
pyramidula Ponsonby & Sykes, 1894: 55 (*Pupa*).
fagoti Westerlund, 1894 (1892–94): 171 (*Pupa*).
sabaudina Locard, 1894: 328 (*Pupa*).
margieri Caziot, 1903: 278 (as var. of *umbilicata* Draparnaud)
(*Lauria*).
?bourbonensis Pilsbry, 1922 (1922–26): 68 (*Lauria* (*Lauria*)).

Shell (Fig. 55) 3.5–5 mm high by about 2 mm in diameter,
from tall cylindrical to stumpy conical, with 6–7 delicately
transversely striated, gradually increasing whorls, yellow-
ish brown to reddish brown, translucent and glossy. Um-
bilicus narrow. Protoconch (Fig. M19) smooth, of about
1.5 whorls, apically flat, without a very shallow suture.
Aperture (Fig. M20) truncate-oval, slightly oblique. Ad-
ults usually with a short, curved angular lamella, with or
without connection to outer lip, continuing inwards as a
thread for about a half whorl. Juveniles (Fig. M21, 22)
with middle parietal and columellar walls bearing lamellae
that penetrate deeply into body whorl, and palatal wall
having a number of radial laminae. Peristome usually re-
flected and thickened, whitish, with a callus thickening at
inner margin.

Animal steely blue to grey dorsally, shading to pale grey at sides and on sole. Tail rather short, not extending behind shell in active animal. Locomotion by muscular pedal waves generated from posterior of sole.

Reproductive system, Fig. 88. Ovotestis comprising a series of single acini opening to proximal hermaphrodite duct, embedded in digestive gland. Hermaphrodite duct rather long, markedly distended and convoluted in middle section, terminating in a multilobate, diverticular talon embedded in albumen gland. Spermiduct and oviduct fused to form spermoviduct; female part proximally slender but for the most part sacculate, in gravid animals greatly distended by embryos; prostatic gland short, fused with proximal female oviduct. Free oviduct and vagina short, stout. Bursa copulatrix reservoir small, bulbous, on a long, slender duct. Vas deferens long and very slender, at its distal end expanding abruptly into an epiphallus which lacks a flagellum. Phallus rather short, thick-walled, bearing apically an elongate caecum armed internally with spinate papillae, and laterally carrying an appendix with a bulbous base giving rise to a glandular sac on a slender duct; entry of epiphallus direct, not through a papilla. Atrium short but distinct.

Spermatophores unknown.

Phallic retractor arising from diaphragm, bifurcating to insert laterally on phallus and on bulbous base of phallic appendix.

Jaw (Fig. 129) about 0.2 mm wide, crescent-shaped, with numerous fused plates.

Radular ribbon (Fig. M95, M96) with about 110 transverse rows of teeth, each of formula 10+2+7+C+7+2+10. Central tooth well developed, tricuspid, with a large mesocone and short ectocones on a quadrate basal plate. Lateral teeth bicuspid, with a large mesocone and a smaller but prominent ectocone, on quadrate basal plate. Teeth transitional between lateral and marginal characterised by bifurcation of ectocone and shortening of basal plate. Marginal teeth with a shortened mesocone and a serrate ectocone (cusps lacking on extreme marginals), on a broad but short basal plate.

Digestive tract, Fig. 158. Buccal mass spheroidal. Oesophagus long, terminating in gastric pouch without any apparent crop formation. Gastric pouch cylindrical, extending about 0.6 of a whorl to end in a sacculate stomach which is not externally differentiated. Intestine producing short, anteriorly and posteriorly directed loops before running as a long rectum to anus in mantle collar.

Pallial complex, Fig. 184. Pulmonary cavity long, extending about 2.25 whorls. Kidney proper short, barely exceeding length of pericardium, extended to about 0.85 of pulmonary cavity length by a slender ureteric pouch. Retrograde ureter absent, but a ciliated groove extending for a short distance from excretory orifice towards top of pulmonary cavity. Pulmonary cavity poorly vascularised.

Free muscle system, Fig. 210. Columellar muscle dividing shortly after its origin into 2 primary branches: left branch to left ocular and inferior tentacles, giving rise to buccal retractors in its middle section; right branch dividing into a well developed, extensively radiating tail fan, and tentacle retractors. Retractor branch to right ocular peduncle passing over phallus.

Central nervous system, Fig. 236. Cerebral commissure length about equal to cerebral ganglion width. Cerebropedal connectives subequal in length, the right one about 1.5x as long as width of cerebral ganglion. Pleural ganglia markedly closer to cerebral ganglia than to pedal ganglia. Parietal ganglia closer to visceral ganglion than to pleural ganglia; right parietal apparently fused with visceral ganglion, which lies to right of median plane.

Type material. The type locality is England. The whereabouts of the type material is unknown.

Distribution. Widely distributed in western Europe and the eastern Atlantic islands, eastwards to the Caucasus and Asia Minor. Introduced into St Helena, Réunion, the U.S.A., Canada, Jamaica, South Africa, and New Zealand.

Recommended common name. Chrysalis snail.

Material examined. New Zealand. ND. Pandora, 12 Mar 1992, A.C. Willoughby. Taipa, 16 Jul 1992, O.J. Marsten, in sand dunes. **AK.** Hotea, 20 Apr 1987, B.F. Hazelwood & H. Taylor. Birkenhead, undated, B.F. Hazelwood, adjacent to motorway. University of Auckland, Auckland central, Jul 1987, S. O'Shea, in gardens. Panmure, 12 Dec 1987, B.F. Hazelwood. Orakei, Little Rangitoto Reserve, 6 Sep 1987, B.F. Hazelwood, in scoria outcrop. Onehunga, 23 Sep 1978, B.F. Hazelwood, under hedge in garden. Glenn Innes, University Park, 6 Sep 1987, B.F. Hazelwood. Mt Eden, 15 May 1987 and 6 Jun 1987, B.F. Hazelwood, in scoria rubble in remnant forest and rock walls. Mt Albert, 8 Jun 1987, B.F. Hazelwood. Mt Wellington, 20 Jun 1987, B.F. Hazelwood. Tamaki, 1 Nov 1993, B.F. Hazelwood. Ellerslie, 4–5 Apr 1987, B.F. Hazelwood & H. Taylor; 12 Jul 1987, 8 Oct 1988, and 17 May 1989, B.F. Hazelwood. Mangere, 20 Jul 1987, B.F. Hazelwood & T. Te Kiro. Manukau, Clover Park, 17 Jan 1988, B.F. Hazelwood. **CL.** Tararu, 3 Dec 1988, in grassy area of coastal cliff. **WO.** Hamilton, 6 Nov 1991 and 27 May 1992, A.M. Spurgeon, in garden. Hamilton, 22 Sep 1994, in garden. **BP.** Papamoa Beach, Sep 1989, Jun 1991, and May 1992, in sand dunes. **NN.** Motueka, 6 Oct 1994, under debris on coastal bank. Nelson, 6 Oct 1994, in litter and grass in park.

Extralimital. England. Birmingham, 1979, coll. & det. R.A.D. Cameron. **Ireland.** Oughterard, Galway, 26 Aug 1990, in rock wall. Glenarm, Antrim, 30 Aug 1990, on coastal limestone cliffs. **Scotland.** Auchincruive, Dumfries & Galloway, 12 Sep 1990, in garden. **Spain.** Santiago de Compostella, Galicia, Apr 1989, in park.

History in New Zealand. This species was first collected in New Zealand by Whitten (1955, 1957) but wrongly assigned to *Pupilla muscorum* (Linnaeus, 1758) (Willan 1977). Whitten's (1955) material was collected from Mt Pleasant, Thames in 1944 and Western Springs, Auckland in 1955. Whitten (1957) noted this species from Parnell, Auckland in 1956. Further specimens from Thames were misidentified as *P. muscorum* by Powell (1979). Willan (1977) and Barker (1982) confirmed the establishment of *L. cylindracea* at several localities in Auckland City.

During the present study *L. cylindracea* has been recorded from numerous localities in the northern North Island and from the Nelson region of the South Island.

Biology. The habitat of *L. cylindracea* is varied, but commonly it is found in rocky or stony sites, on walls, in crevices of tree stumps, under bark of fallen trees, and in coastal grassland. In Britain *Lauria* is common in woodland, rocky open areas, and grassland (e.g., Cameron & Redfern 1972, Chatfield 1975, Rouse & Evans 1994). *L. cylindracea* has not been found in areas of native forest in New Zealand.

Ovoviviparous. Gravid animals have been collected in New Zealand from late spring to autumn.

Remarks. The shell form of the species established in New Zealand is clearly that which would be assigned to *L. cylindracea* in Europe, but the anatomy of the dissected series (from Auckland and Hamilton) differs in detail from that described for *L. cylindracea* by Steenberg (1925): (a) the acini of the ovotestis are not clustered into several lobes, but arise singly along the proximal hermaphrodite duct; (b) the hermaphrodite duct does not terminate in a small bulbous talon, but at the base of a large, sacculate and multilobate receptacle; (c) the bursa copulatrix reservoir does not lie against the prostatic gland follicles but more distally, against the sacculate part of the oviduct, indicative of a shorter bursa copulatrix duct; (d) rather than being shorter, the phallic caecum extends the length of the epiphallus; and (e) rather than about 4x, the total length of the phallic appendix exceeds that of the epiphallus by about 2x. The relative portions of the epiphallus, phallic caecum, and phallic appendix are similar in the material described and illustrated by Steenberg (1925) and Schileyko (1975, 1984). However, Schileyko's material differed from Steenberg's and the present New Zealand material in that the phallial branch of the phallic retractor muscle was inserted on the distal epiphallus near the base of the phallic caecum, rather than laterally on the proximal phallus, and the bursa copulatrix duct arose very close to the atrium, resulting in a very short vagina or none, rather than more proximally with a distinct vagina.

This varied combination of character states suggests the possibility of a sibling species complex within what at present is known as *L. cylindracea*. Any analysis of this complex would necessarily include the other common European species *L. sempronii* (de Charpentier, 1837), the typical form of which is indistinguishable from *L. cylindracea* from non-calcareous soils or dry habitats (Manganelli *et al.* 1990).

Entry into the literature on *L. cylindracea* is provided by Pilsbry (1922–26), Germain (1930), Likharev & Rammel'meier (1952), Giusti (1973), Backhuys (1975), Schileyko (1975, 1984), and Manganelli *et al.* (1990).

Family TESTACELLIDAE

Diagnosis. Carnivorous slugs. Shell small, auriform, situated at posterior end of body, covering the pallial organs but not capable of housing retracted animal. Dorsum with a pair of branched lateral grooves arising from prepallial groove and running forwards. Ocular peduncles not bulbous at apex. Caudal mucus pit absent. Sole uniform. Suprapedal gland lying free in body cavity. Jaw absent. Buccal bulb much enlarged, containing radula with V-shaped rows of barbed aculeate teeth, protrusible for impalement and capture of earthworms and other prey, and with strong posterior and (usually) lateral retractor muscles. Intestine reduced in length, describing a broad, anteriorly directed loop before running to anus at mantle collar. Kidney with a short secondary ureter. Genital orifice near base of right ocular peduncle. Genitalia without accessory glands, but phallus with a small diverticulum and an apical flagellum. Right ocular retractor passing forwards over phallus. Cerebral commissure very short; cerebropleural and cerebropedal commissures moderately long.

Haploid chromosome number 32.

Remarks. The family is represented by a single genus native to the western Palaearctic region.

Genus *Testacella* Draparnaud

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Testacella Draparnaud, 1801: 116, type species *Testacella haliotidea* Draparnaud, 1801, by monotypy. (Not *Testacella* of de Monet de Lamarck, 1801 (nude name) [ICZN Opinion 335, 1955a: 58, 59].)

Daudebardia of authors. (Not *Daudebardia* of Hartmann, 1821, type species *Helix rufa* Draparnaud, 1805, by monotypy; Daudebardiidae.)

Diagnosis. Characters as for family.

Testacella haliotidea Draparnaud

Figures 56, 57, 89, 159, 185, 211, 237, C25, M97–99; Map 22

haliotidea Draparnaud, 1801: 116 (*Testacella*).
europaea de Roissy, 1805: 13 (*Testacella*).
galliae von Oken, 1816 (1815-16): 95 (*Testacella*).
maugei of authors (not of d'Audebard de Férussac, 1819).
novae-zealandiae of authors (not Pfeiffer, 1862).
?vagans Hutton, 1882a: 282 (*Testacella*).
barcinonensis Pollonera, 1888: 4 (*Testacella*).
dubia Pollonera, 1888: 4 (*Testacella*).
esserana Fagot, 1892: 32 (*Testacella*).
anomala Torres Minques, 1924: 113 (*Testacella*).

Extended animal (Fig. 56) 80–120 mm long, with small external shell carried over pallial organs at posterior apex of body. Two very distinct grooves, about 2 mm apart at their origin, arising from anterior edge of mantle and describing a lateral arc over back, one on either side, before converging near body anterior. Body usually dull greyish brown to yellow, with pale yellow-white foot fringe and sole. Mucus clear.

Shell (Fig. 57) to 7x5 mm, convexly auriform, subtriangular, with brown periostracum often abraded. Dorsal surface with distinct growth lines. Ventral surface with a crescentic muscle scar. Protoconch vestigial but nonetheless distinct on right aspect of shell posterior apex. Columella expanded to a rounded callus posteriorly, and usually slightly truncate anteriorly.

Reproductive system, Fig. 89. Ovotestis pale, at apex of visceral mass between lobes of digestive gland. Hermaphrodite duct long, slender, much folded, with a bulbous talon at its termination in large albumen gland. Spermoviduct much folded. Free oviduct very short, stout. Bursa copulatrix reservoir oval to spherical, on a short, rather stout duct. Vagina of moderate length, narrowing towards atrium. Vas deferens long and slender, inserted without a papilla at apex of phallus, adjacent to flagellum. Phallus (and its flagellum) slender and tubular, with a small mediolateral caecum, and internally with numerous conical papillae.

Spermatophore unknown, probably not produced.

Phallus retractor long, slender, arising from dorsal body wall at hind end of body cavity and inserted at apex of phallus.

Radular ribbon (Fig. M97–99) of about 50 V-shaped rows of teeth, 18 teeth on either side of midline. Central tooth usually absent, occasionally vestigial. Teeth barbed aculeate, each with a vestigial mesocone midway between base and apex, gradually increasing in size up to the penultimate one; marginal (18th) tooth shorter.

Digestive tract, Fig. 159. Buccal mass large, cylindrical. Oesophagus short. Crop thick-walled, cylindrical, merging with thick-walled stomach at level of posterior limit of buccal mass, conspicuously connected with dorsal and lateral body wall by a number of thin muscle strands. Intestine arising from left lateral aspect of stomach, forming a broad anteriorly directed loop before running to anus at right posterior of body.

Pallial complex (Fig. 185) at posterior of body, overlain by shell and mantle. Kidney rectangular, lying below and largely in front of pulmonary chamber, opening into a very short ureteric tube. Pulmonary chamber a thin-walled air sac. Heart in pericardium on right side of kidney, with ventricle in front of auricle; aortic stem extending forwards beyond pallial complex before branching. Osphradium in floor of pulmonary chamber, comprising a ridge of cells innervated from visceral ganglion.

Free muscle system, Fig. 211. Ocular retractors arising asymmetrically from lateral body wall a little anteriad of pallial complex; right retractor arising from pedal musculature and passing between phallus and vagina. Buccal retractor arising from left posterior body wall, inserted laterally on left side of buccal mass as numerous muscle bundles.

Central nervous system, Fig. 237a, b. Cerebral ganglia appressed, united by a very short and indistinct commissure. Right cerebropedal connectives slightly longer than those on the left, their length about equal to width of cerebral ganglion. Pleural ganglia close to pedal ganglia, to which they are linked by short connectives. Visceral chain compact; parietal ganglia closely appressed to pleural ganglia; visceral ganglion to left of median plane, closely appressed to left parietal ganglion and linked to right parietal ganglion by a very short connective.

Haploid chromosome number 32.

Type material. Represented by two syntypic specimens in NHMW (Acq. No. 1820. xxvi. 151). The type locality is assumed to be Montpellier, France.

Distribution. Naturally distributed in the Western Palaearctic region from the Atlantic isles to the Balkans, and from the North African coast to southern Scotland. Introduced into Canada, the U.S.A., Cuba, Australia, and New Zealand.

Recommended common name. Shelled slug.

Material examined. New Zealand. AK. Auckland, shells only, T.F. Cheeseman (CMNZ M352, lectotype, and CMNZ

5033, syntypes (2) of *Testacella vagans* Hutton, 1882). Mt Eden, shell only, R.K. Dell (MONZ). **GB**. Waihirere, 21 Jun 1978, A.C. Firth, in pasture. Gisborne, 30 Aug 1991, K.B. Taylor. **HB**. Napier, 27 Sep 1978 and 1 Nov 1978, R.F. Lowe, in vegetable garden.

History in New Zealand. Testacellid slugs were first recorded for New Zealand as *Daudebardia novoseelandica* (not of Pfeiffer) by Hutton (1881), and later described as a new species, *Testacella vagans*, by Hutton (1882a). Musson (1891), Suter (1891), and Hedley (1892) correctly pointed out that Hutton's slug was a naturalised species, possibly *T. maugei* d'Audebard de Férussac. Subsequently *T. maugei* appeared regularly in listings of molluscs introduced into New Zealand. Recorded localities were Ashburton and Nelson (South Island), Waiuku and Auckland (North Island).

Although the type specimen of Hutton's slug had not been traced and hence could not be examined, I earlier (Barker 1979) listed *T. vagans* in the synonymy of *T. haliotidea*, primarily on the basis of radular form. Shell material collected in Mt Eden, Auckland and deposited in MONZ by R.K. Dell during the 1950s was referred to *T. maugei* by Whitten (1955), but appears to be of *T. haliotidea* (Barker 1979). However, Hutton's type material was discovered in CMNZ during the present study. The form of the lectotype and (2) syntype shells of *T. vagans* indicates that this taxon is conspecific with *T. maugei*. It remains uncertain as to whether both *T. maugei* and *T. haliotidea* have established in the Auckland area, where no testacellid slugs have been seen for at least 35 years.

During 1978 and subsequently, testacellid slugs have been collected on a number of occasions from localities in the Poverty Bay and Hawkes Bay regions of the North Island. Dissections of preserved animals (Barker 1979 and this study) have shown these to be *T. haliotidea*.

Biology. *Testacella* is largely synanthropic in Britain (Kerney 1966), and primarily subterranean in gardens and other cultivated soils. During the day the slugs remain underground, emerging at night to prey upon earthworms, slugs, snails, and other soil animals such as centipedes on the soil surface. Feeding behaviour and the function of the buccal mass in *Testacella* has been described by de Lacaze-Duthiers (1887), Webb (1893), Taylor (1902–07 (1902–21)), Barnes (1950), Barnes & Stokes (1951), and Crampton (1975). During dry or particularly cold weather *T. haliotidea* retreats into the soil to depths often greater than 1 metre. Under these conditions the slugs may go into a form of aestivation in earthen cells lined with viscid mucus.

Because of their subterranean habit, testacellid slugs are rarely observed, and hence little is known of their bionomics. According to Taylor (1902–07(1902–21)) and Barnes & Stoke (1951) the slugs are most active in spring and autumn, when mating occurs either in the soil or under cover on the soil surface. Copulation lasts for 4 or 5 hours. Chemin (1939a, b) reported self-fertilisation in *T. haliotidea* isolated when young. Eggs are ellipsoidal, 7x4 mm, with a calcareous shell which changes from white to yellow, and are deposited in clusters deep in the soil. Gassies (1849) reported that eggs took 10–22 days to hatch, while Barnes & Stokes (1951) recorded development times of 144–201 days. According to Taylor (1902–07 (1902–21)), *Testacella* takes about 18 months to reach sexual maturity, and may live for 5 or 6 years.

Remarks. Many old records of *T. haliotidea* can be referred to *T. scutulum* Sowerby, 1821, as the latter was considered by many authors to be only a variety of *T. haliotidea*, and was not distinguished in the literature.

Several variety names of *T. haliotidea* appear in the literature, based on variation in shell characters and body coloration (e.g., Quick 1960).

Entry into the European literature pertaining to *T. haliotidea* are provided by Germain (1930), Quick (1960), Diaz *et al.* (1986), and Martin & Rallo (1986).

Family VALLONIIDAE

Diagnosis. Herbivorous holopod snails, oviparous or ovoviviparous. Shell cylindriform, low-conical, or turbinate, less than 5 mm in height, umbilicate, sometimes with periostracal ribs or processes, frequently with aperture barriers, capable of fully housing the retracted animal. Animal lacking inferior tentacles in some taxa. Sole uniform, without a caudal mucus pit. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw aulacognathic. Radula with marginal teeth multicuspid, on broad, short basal plates. Intestine with a single loop directed forwards. Kidney very elongate, divided internally into 2 distinct regions, the anterior region functioning as a primary ureter; secondary ureter absent except in *Acanthinula*, which has a short, closed retrograde duct. Columellar muscle branching at or a short distance from origin into left and right cephalic retractor bundles; buccal retractor associated with left branch, tail fan associated with right branch. Right ocular retractor crossing phallus. Genital orifice near right ocular peduncle, or sited on visceral stem near pneumostome. Spermoviduct formed; prostatic gland short, confined to proximal pallial gonoduct in ovoviviparous forms, longer in oviparous forms. Bursa copulatrix

duct of moderate length or rather short, in some taxa with a diverticulum. Aphally common; male genitalia (when present) with an epiphallus and phallus equipped with a well developed appendix and gland; phallus frequently with an apical caecum. Phallus retractor muscle arising from diaphragm, bifurcating to insert on phallus and its appendix. Cerebropedal connectives frequently subequal in length but never long. Right pleural ganglion closer to right cerebral than to right pedal ganglion. Visceral ganglion chain moderately concentrated, on right of median plane.

Haploid chromosome number 28.

Remarks. The limits of the Valloniidae and their affinities to other orthurethran families have not been fully resolved. Zilch (1959–60) and Tillier (1989) divide the nominal family into several subfamily taxa: Valloniinae, Acanthinulinae, Strobilopsinae, and Spelaeodiscinae. The Valloniidae in this sense are closest to the Achatinellidae, Pupillidae, and Pyramidulidae in Tillier's (1989) classification. Pilsbry (1948 (1939–48)) and Giusti & Manganelli (1986) question the validity of the current subfamily divisions of the Valloniidae. I have therefore used Valloniidae in the broad sense of Zilch and Tillier, without recognition of subfamily units. In this sense the family is represented by 15 extant genera.

The Valloniidae are widely distributed in temperate and tropical regions, and are represented in New Zealand by a single naturalised species.

Genus *Vallonia* Risso

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Zurama Leach, 1819: 108, type species *Helix pulchella* Müller, 1774 [= *V. pulchella* (Müller, 1774) + *V. castata* (Müller, 1774)], by original designation.

Vallonia Risso, 1826: 101, type species *Vallonia rosalia* Risso = *Vallonia pulchella* (Müller, 1774), by monotypy [ICZN Opinion 335, 1955a: 50, 59]. See Pilsbry (1948(1939–48)) for comment on identity of Risso's *V. rosalia*.

Amplexis Brown, 1827: figs 76 & 77, type species *Helix paludosus* da Costa = *V. pulchella* (Müller, 1774), designated by Pilsbry (1927–35); amended to *Amplexus* by Brown (1844 (1837–49)). (Not *Amplexus* of Sowerby, 1814; Cnidaria.)

Chilostoma of authors. (Not *Chilostoma* of Fitzinger, 1833, type species *Helicigona zonata* Studer, 1820 = *Helicigona foetens* Studer, 1820, designated by Gray (1847); Helicidae.)

Circinaria Beck, 1837 (1837–38): 23 (as subgenus of *Helix* Linnaeus, 1758), type species *Helix pulchella* Müller, 1774, designated by Herrmannsen (1847).

Corneola of authors. (Not *Corneola* of Held, 1837 (1837–38), type species *Helix cornea* Draparnaud, 1801, designated by

Herrmannsen (1847) – synonym of *Chilostoma* Fitzinger, 1833; Helicidae.)

Lucena Gray, 1840: 142, type species *Helix pulchella* Müller, 1774, designated by Moquin-Tandon (1855).

Glaphyra Albers, 1850: 87, type species *Helix pulchella* Müller, 1774, designated by Pilsbry (1927–35).

Planivallonia Schileyko, 1984: 170, type species *Vallonia zaru* Almuhambetova, 1979, by original designation.

Diagnosis. Shell depressed, helicoid, broadly umbilicate; peristome continuous or nearly so, thickened and reflected, in some species with periostacal ribs; aperture always lacking teeth. Animal with inferior tentacles. Oviparous. Bursa copulatrix duct short, lacking a diverticulum. Genital orifice well posterior of right ocular peduncle, at base of visceral stalk. Central nervous system with left pleural and parietal ganglia closely appressed; right parietal ganglion fused with visceral ganglion.

Haploid chromosome number 28.

Remarks. Gerber (1996) recognised 40 species and subspecies in *Vallonia*. The genus has a wide distribution in Europe, North Africa, Atlantic islands, North America, North and Central Asia, and Japan. Several species have been dispersed by human commerce.

Vallonia excentrica Sterki

Figures 58, 90, 130, 160, 186, 212, 238, 253, C26, M23, M100, M101, M119, M120; Map 23

pulchella of authors (not of Müller, 1774).
? paludosa da Costa: 1778: 59 (*Helix*).
excentrica Sterki, 1893a: 249 (*Vallonia*).
excentricoides Weiss, 1894: 151 (as var. of *pulchella* Müller) (in error for *excentrica* Sterki) (*Vallonia*).

Shell (Fig. 58) to 1.2 mm high by 2.3 mm in diameter, with 3–3.5 rapidly increasing rounded whorls, the last quarter-whorl expanding noticeably, whitish or straw coloured, somewhat translucent. Protoconch (Fig. M23) with slight roughness and lined by numerous thin spiral grooves. Teleoconch furnished with growth lines, as well as rare, weak traces of irregularly disposed and branched periostracal striae. Umbilicus open, elliptical, about 0.25 of shell diameter. Aperture circular, rather oblique and inclined. Peristome not continuous, abruptly thickened to form a white lip but weakly reflected.

Animal translucent white. Tail in active animal very short. Sole undivided, narrow, with margin weakly crenulate; progression by advancing muscular waves. Genital orifice at base of visceral stalk.

Reproductive system, Fig. 90. Ovotestis embedded in digestive gland, composed of 3 clusters of 3–5 acini. Her-

maphrodite duct slender and straight proximally, much swollen and contorted in middle part, before again becoming slender to run to an elongate talon with bulbous head. Female pallial gonoduct sacculate, especially immediately below that part fused with prostatic gland. Free oviduct rather short. Bursa copulatrix reservoir oval, on a rather short duct. Vagina moderately long. Prostatic gland with elongate follicles, confined to proximal pallial gonoduct, where it fuses with female tract to form a spermoviduct. Vas deferens long and slender. Epiphallus arched, dilated at entry to phallus, where it houses a short conical papilla. Phallus comprising a rather sacculate proximal part and short tubular distal part, the lumen of both lined with low folds; an appendix arising from proximal phallus, with a bulbous base, housing a fleshy, elongate papilla, giving rise to a glandular sac on a slender stem. Atrium short, indistinct. Male terminal genitalia often absent.

Spermatophores unknown.

Phallus retractor arising from anterior part of diaphragm, bifurcating to attach to medial part of epiphallus and basal part of phallus appendix.

Jaw (Fig. 130) arcuate, 0.23–0.25 mm wide, sculptured with 18–26 low folds which denticulate the margin, often with a slight median projection.

Radular ribbon (Fig. M100, 101) with 70–77 transverse rows of teeth, each varying around the formula 10–12+3–4+C+3–4+10–12. Central tooth narrower than adjacent laterals, tricuspid, with mesocone not half as long as rectangular basal plate. Lateral teeth bicuspid with basal plates squarish; mesocone large, in length equal to or exceeding basal plate height; ectocone small. Marginal teeth multicuspid, on broad but short basal plates.

Digestive tract, Fig. 160. Buccal mass spheroidal. Oesophagus long, slender, terminating in a gastric pouch without crop formation. Gastric pouch inflated, cylindrical, extending about 0.3 of a whorl to merge with sacculate stomach, which is not externally differentiated. Intestine producing long anteriorly and posteriorly directed loops, then running to anus at mantle collar.

Pallial complex, Fig. 186. Pulmonary cavity rather short, extending about 0.6 of a whorl. Kidney short, barely exceeding length of pericardium, extended to about 0.9 of pulmonary cavity length by a conical ureteric pouch. Retrograde ureter absent, but a ciliated groove extending for a short distance from anterior excretory pore towards top of pulmonary cavity. A spongy tissue mass overlying rectum immediately before anus.

Free muscle system, Fig. 212. Columellar muscle dividing at origin into a left cephalic bundle and a right, short but broad tail fan. Cephalic bundle dividing into left and right branches, which each run to ocular peduncles, inferior tentacles, and anterior body wall. Buccal retractor

arising from left branch of cephalic retractor. Right ocular retractor passing between male and female branches of terminal genitalia.

Central nervous system, Fig. 238. Cerebral commissure rather short, its length less than cerebral ganglion width. Length of cerebropedal connectives exceeding width of cerebral ganglia; left connective slightly longer than the right. Right pleural ganglion closer to cerebral ganglion than to right pedal ganglion; left pleural ganglion sited midway between left cerebral ganglion and pedal ganglion. Left parietal ganglion separated from both left pleural ganglion and visceral ganglion by short connectives, but closer to the former. Right parietal ganglion separated from right pleural by a short connective, but fused to visceral ganglion, which lies to right of median plane.

Chromosome numbers unknown.

Type material. Described from Staten Island, New York, U.S.A. (see Pilsbry 1948 (1939–48), p. 1025).

Distribution. Apparently native to the Mediterranean, western Europe, Atlantic islands, and North America. Introduced to St Helena, South Africa, Australia, and New Zealand.

Recommended common name. Eccentric grass snail.

Material examined. New Zealand. Kermadec Is. Raoul I., Mt Campbell, Dec 1997, T. McGluggago. Raoul I., Expedition Hill, Dec 1997, T. McGluggago. **ND**. Tapotupotu Bay, 13 Nov 1979, B.F. Hazelwood. Kaitaia, 1986, in pasture. South Mangatu State Forest, 6 Mar 1977, B.F. Hazelwood (MONZ M55761). Ngungura, Jul 1978, P.C. Mayhill (MONZ M58144). Waro, B.F. Hazelwood, in limestone outcrop. Whangarei, Tikipunga, Oct 1991, A. Spurgeon. Tokatoka, Jan 1982, P.C. Mayhill. **AK**. Te Hana, 23 Feb 1994, in pasture. Leigh, 5 Dec 1979 and 18 Mar 1989, B.F. Hazelwood. Woodcocks, Jul 1988, B.F. Hazelwood. South Kaipara Heads, 1987, R.N. Wrenn, in pasture. Hobsonville RNZAF, Dec 1980, P. Sudlow (MONZ M70750). Glenfield, 20 Feb 1988, B.F. Hazelwood. Glen Innes, University Park, 6 Sep 1987 and 21 Dec 1987, B.F. Hazelwood. Titirangi, 26 Sep 1983, B.F. Hazelwood. Mt Wellington, 22 Dec 1987, B.F. Hazelwood. Ellerslie, 4 Apr 1987, 24 Oct 1987 and 3 Mar 1989, B.F. Hazelwood. Onehunga, 23 Sep 1978, B.F. Hazelwood. Whitford, Puhinui, undated, R.K. Dell (MONZ M5386). Papatoetoe, undated, W. Ponder (MONZ M20541). **CL**. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in grass at roadside. Thames, Oct 1988, in park lawn. **WO**. Onewhero, Mar 1987, in pasture. Limestone Downs, 13 Feb 1981, F.M. Climo & D.J. Roscoe (MONZ M77936). Tahuna, 25 May 1976, in pasture. Ohinewai, 18 Jul 1977, in pasture. Waikaretu, 17 Sep 1977, B.F. Hazelwood (MONZ M57338). Taupiri, 18 Jul 1977. Tatuanui, Sep 1981, in pasture. Ngaruawahia, 1977, C. Broomfield (MONZ M57905). Tauwhare, 22 Feb 1995, in pasture. Te Miro, 19 Apr 1977, in grassy area at roadside. Hamilton, 22 Jun 1977, 24 Sep 1978, and

20 Dec 1978, in lawn. Matangi, 6 May 1977, H. Oliver, in pasture. Matamata, Aug 1984, in pasture. Rukuhia, May 1977 and May 1983, in pasture. Te Uku, 16 Jul 1977, in pasture. Whatawhata, 8 Sep 1977 and 23 Dec 1993, in pasture. Cambridge, Jul 1978, in park lawn. Ohaupo, 12 May 1980, in pasture; Jul 1991, in pasture and lawn. Pirongia, 19 Sep 1978, in pasture. Tirau, Oct 1979. Pokuru, Oct 1974, in pasture. Waikeria, 31 May 1977, in pasture. Pukeatua, Apr 1992, in grassy area at margin of *Beilschmiedia tawa* forest. Lichfield, Sep 1974, in pasture. Waitomo, Mar 1977, P.C. Mayhill, limestone outcrops in pasture and open remnant *Beilschmiedia tawa* forest at 340 m; 3 Mar 1977, 19 Sep 1978, and 8 Dec 1978, in pasture; 16 Nov 1977, K. Brown (MONZ M85416). Mairoa, Aug 1979, in pasture; Te Kuiti, Aug 1978. Mahoenui Valley, Totara Rd Cave, 5 Mar 1977, F.M. Climo (MONZ M56837). **BP.** Tauranga, Apr 1956, M. Hodgkins (MONZ M9795); 1984, B. McFadgen, archaeological survey (MONZ M86077). Otumoetai, 26 Dec 1988, B.F. Hazelwood. Manawaru, Sep 1981, in pasture. Te Puke, Apr 1977, in pasture. Lower Kaimai, 25 Jun 1977, in pasture. Ohiwa, Kutarere, 15 Jan 1976, B.F. Hazelwood, in shell sand. Opotiki, Oct 1988, in pasture. Waimana, Oct 1988, in pasture. Waioeka, Oct 1988, in pasture and grassy area at road-side. Waikawa, Oct 1988, in pasture. Hicks Bay, 23 Sep 1992, in coastal broadleaf scrub. **GB.** Tuparoa, Oct 1988, in pasture. Tokomaru Bay, Mata River, 14 May 1983, F.M. Climo (MONZ M78207). Gisborne, Kaiti Beach, 26 Feb 1950, R.K. Dell (MONZ). **TO.** Rainbow Mountain, Mar 1980, P.C. Mayhill. Reporoa, 13 Jul 1993, in pasture. Broadlands, Sep 1986, in pasture. Ongarue, Dec 1977. **TK.** New Plymouth, Brooklyn Bush, Nov 1981, P.C. Mayhill. **HB.** Tangoio, Devils Elbow, 1 Jan 1977, B.F. Hazelwood (MONZ M56282). Waimarama, 8 Mar 1977, B.F. Hazelwood (MONZ M55721). **WN.** Otaki, undated, B.F. Hazelwood. Pukerua Bay, Wairaka Point, 23 Feb 1958, D.P. Fairfax (MONZ M12076). **NN.** Clifton, The Grove, Jan 1973, R.E. Fordyce (MONZ M37323). Takaka Saddle, Oct 1979, P.C. Mayhill. Takaka Hill, 4 Jun 1977, B.F. Hazelwood (MONZ M69930); Oct 1979, P.C. Mayhill (MONZ M67919); Feb 1981, P.C. Mayhill, 750 m. Tahunanui, Apr 1952, R.A. Cumber (MONZ). Nelson, 20 Mar 1939, E.S. Gourlay (MONZ). Stoke, Feb 1962, S. Greenwood (MONZ M15323).

Extralimital. England. Hurley, Berkshire, 12 May 1990, in pasture. Lyme Regis, Sep 1990, in grassy area at coast. **U.S.A.** Rock Springs, Pennsylvania, May 1994, in pasture.

History in New Zealand. Crosse (1893) recorded *V. pulchella* (Müller, 1774) from New Zealand, without collection data. In the same year Suter (1893b) listed *V. pulchella* as having been found in Albert Park, Auckland by Cheeseman. This record apparently formed the basis of Suter's (1913) listing of *V. excentrica* from Auckland. In addition to listing Taranaki as a new locality for *V. excentrica*, Thomson (1922) referred to records of *V. pulchella* from Auckland by Musson (1891), who however does not list any New Zealand localities for *V. pulchella*. It would seem that Crosse (1893) was in error in thinking that Musson had recorded *Vallonia* from New Zealand, and that

this error was subsequently repeated by Thomson (1922). Unless shown otherwise by material in the collections of Musson, the first authentic record of *Vallonia* in New Zealand (specifically, *V. excentrica*) is that of Suter (1893b).

Whitten (1955) lists Leigh, Auckland, Taranaki, and Nelson (incl. Tahunanui) as localities for *V. excentrica*. Whitten (1957) added Papakura and Taipa Beach as localities. This pattern of widespread distribution in the North Island and restriction to the Nelson region in the South Island is confirmed by Barker (1982 and this study).

Whitten (1957) recorded *V. costata* (Müller) from Devonport. I have not been able to confirm the presence of this species in New Zealand.

Biology. *Vallonia excentrica* is a xerophile, common in grasslands (e.g., Boycott 1934, Kerney 1966, Cameron & Redfern 1972, Rouse & Evans 1994). Kerney & Cameron (1979) give its habitat as "open, usually dry calcareous places: short-turfed grassland, screes, sand-dunes; not normally in woods or marshes." This applies equally to New Zealand, except that the species occurs in pastures over a wide range of soil acidity (pH 4.5–7) and thus is not restricted to calcareous sites. *V. excentrica* has become a conspicuous element of the pasture fauna on many northern New Zealand soils. Barker (1985) provided information on its biology in two Waikato pastures, which suggested that dispersion and abundance are governed by microclimatic factors such as drainage.

V. excentrica displays deterministic growth. Barker (1985) found that under favourable conditions the snails grow steadily until maturity when peristome thickening occurs in shells of 2–2.4 mm diameter. In the laboratory, snails took an average of 48 days at 25°C to attain maturity. Snails commenced oviposition within 7 days of peristome thickening, producing an egg every 1–3 days (mean 0.86 eggs per day) when first reproductive. After several months both oviposition rate and egg viability declined, when the spent snails died. Analysis of population census counts taken from Waikato pastures, where abundance as high as 1500 per m^2 was recorded, indicated that two generations occur each year, with recruitment in spring to early summer and in late summer to autumn.

Watson (1920) found English examples of *V. excentrica* and *V. pulchella* to be aphallic. In contrast, among 45 specimens of *V. costata* examined by Watson, 3 were euphallic and 42 were aphallic. Giusti & Manganelli (1986) maintain that constant aphally is a character of the *pulchella* group, in which they include *V. excentrica*. Both euphallic and aphallic individuals are represented in New Zealand populations of *V. excentrica*; this apparently is the first report of euphally in *V. excentrica*. In a sample from Waikato pastures dissected by Barker (1985), 29 were

found to be aphallic and 7 euphallic. Dissection of a larger sample assembled from other New Zealand localities during the present study indicated a similar incidence of dimorphism (n = 45: 37 aphallic, 8 euphallic), although several sites yielded exclusively aphallic specimens.

Copulation (Fig. 253) in euphallic *V. excentrica* was observed by Barker (1985). The mode of reproduction in aphallic individuals is not known. Boycott (1917) suggested cross-fertilisation by vaginal copulation between aphallic forms of *Acanthinula* Beck, 1847 and *Spermodea* Westerlund, 1902. Watson (1934) noted that structural differences in genitalia suggest that the euphallic forms reproduce by cross-fertilisation and aphallic forms by self-fertilisation. In discussing male copulatory organ deficiency in Stylommatophora, Riedel (1953) suggested alternative reproductive modes: (1) vaginal coupling between aphallic forms; (2) copulation between a euphallic individual, functioning as a male, and an aphallic individual, functioning as a female; or (3) aphallic forms reproducing without copulation, by parthenogenesis or self-fertilisation. Whitney (1938) has documented self-fertilisation and production of fertile progeny in *V. pulchella* isolated from birth.

Eggs of *V. excentrica* are deposited singly on the soil surface, usually amongst plant litter. They vary from spherical, 0.65 mm in diameter, to slightly flattened spheroids 0.7x0.65x0.58 mm. As in all *Vallonia* species (see Tompa 1976), a brittle shell (Fig. M119, 120) of calcite crystals imparts a pure white appearance to the eggs. From laboratory studies Barker (1985) estimated that approximately 148 degree-days above a threshold of 10°C is required for complete embryo development and egg hatch. Barker (1985) recorded high mortality of *V. excentrica* in Waikato pasture during the egg stage, especially during autumn. Whitney (1938), working with *V. pulchella*, found the eggs to be very sensitive to desiccation.

Remarks. The specific distinction between *Vallonia pulchella* Müller, 1774 and *V. excentrica* Sterki, 1893 has been the subject of debate for many years. Some authors (e.g., Wagner 1935, Hubendick 1950, 1952, 1953, Jacobson 1950, Varga 1972, Giusti 1976) consider *excentrica* to be merely an ecological variant of *pulchella*. Other authors (e.g., Kuiper 1951, Mandahl-Barth 1951, Sparks 1953, Hubricht 1969) have presented evidence in favour of *excentrica* being recognised as a distinct species. This latter view has been accepted by most authors over the past few decades. Giusti & Manganelli (1986) argue that the present *Vallonia* taxonomy, founded on weak conchological peculiarities, is rather subjective. They hold that the high frequency of aphally ('constant aphally', in their wording) in the *pulchella* group suggests an aggregation of genetically distinct entities whose affinities are not distinguishable on a morphological basis.

In the most recent revision of the genus, Gerber (1996) treated *V. excentrica* as a species distinct from *V. pulchella*. I have used *excentrica* for the populations naturalised in New Zealand, in the hope that the status of this entity may be resolved at some later date, perhaps by molecular techniques. Because many early authors did not distinguish between these entities, earlier references to *V. pulchella* may in fact refer to *V. excentrica*.

Entry into the literature on *V. excentrica* is provided by Pilsbry (1948 (1939–48)), Hubendick (1950, 1953), Sparks (1953), Bequaert & Miller (1973), Backhuys (1975), Grossu (1987), and Gerber (1996).

Family VERTIGINIDAE

Diagnosis. Herbivorous holopod snails. Shell dextral or sinistral, under 5 mm in height, ovate, ovate-cylindrical, cylindrical, or exceptionally cylindric-conical or spindle-shaped, capable of housing retracted animal; aperture simple or armed with barriers formed at sexual maturation. Animal often lacking inferior tentacles. Sole undivided; progression by pedal waves initiated from posterior. Caudal mucus pit lacking. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal. Jaw aulacognathic. Radula with marginal teeth multicuspid, on broad but short basal plates. Intestine with a single loop directed forwards. Kidney very long, divided internally into 2 distinct regions, the anteriormost functioning as a primary ureter; secondary ureter lacking. Columellar muscle dividing at or a short distance from origin into left and right cephalic retractor bundles; buccal retractor associated with left branch, tail fan with right branch. Right ocular retractor crossing phallus. Phallus retractor arising from diaphragm, undivided or bifurcate. Genital orifice a short distance behind ocular peduncle. Bursa copulatrix reservoir on a long duct. Epiphallus simple, without a flagellum, or absent. Phallus with or without appendages; aphally evident in some species. Central nervous system with moderately long cerebropedal connectives. Pleural ganglia closer to cerebral ganglia than to pedal ganglia. Visceral ganglion chain moderately concentrated.

Chromosome number unknown.

Remarks. The Vertiginidae *sensu* Zilch (1959–60), inhabiting North America, Eurasia, North to Central Africa, and northern Australia.

As pointed out by Pokryszko (1990a), the systematic position of the majority of taxa classified with the Vertiginidae is obscure, as members of only 9 of the 16 genera have been studied anatomically. Pokryszko proposed restriction of the Vertiginidae to the genera *Vertigo* Müller, 1774, *Truncatellina* Lowe, 1852, and *Columella* Westerlund, 1878, with provision for inclusion of other genera should anatomical investigation show that they too are characterised by the simple structure of the copulatory organs. In the present work Zilch's (1959–60) definition of Vertiginidae is used, with the simple male genitalia taken as a diagnostic character at the subfamily level.

Fusion of the right parietal ganglion with the cerebropedal connective noted by Tillier (1989) in the central nervous system of *Bothriopupa breviconus* Pilsbry, 1917 (Truncatellininae) and *Sterkia eyriesii* (Drouet, 1859) (Nesopupinae) are not apparent in *Vertigo*. In the *Vertigo* species considered here and *V. moulinsiana* (Dupuy, 1849) examined by Steenberg (1925), the nervous system is characterised by the five ganglia of the visceral chain being distinct and the left cerebropedal connective being longer than the right. These differences have been incorporated into the diagnoses presented here, but further anatomical study of Vertiginidae is warranted.

Subfamily VERTIGININAE

Diagnosis. Oviparous snails. Shell dextral or sinistral, less than 3 mm high; aperture armed with 1–11 barriers, exceptionally simple, its margin in adults thickened. Animal lacking inferior tentacles. Prostatic gland small, comprising one to several processes, fused to female pallial gonoduct to form a short spermoviduct. Epiphallus present. Phallus retractor undivided, inserted on apex of epiphallus. Male terminal genitalia without accessory organs. Central nervous system with right cerebropedal connective slightly shorter than the left, and ganglia of visceral chain not fused.

Remarks. Represented by a single genus, *Vertigo* Müller, 1774, with about 100 species widely distributed in the Holarctic region.

Genus *Vertigo* Müller

Vertigo Müller, 1774: 124, type species *Vertigo pusilla* Müller, 1774, by monotypy [ICZN Opinion 335, 1955a: 50, 59].

Pupa of authors. (Not *Pupa* of Röding, 1798, type *Pupa grisebia* Röding, 1798 = *Voluta solidula* Linnaeus, 1758, designated by Suter (1913) – synonym of *Solidula* Linnaeus, 1758;

Acteonidae. Not *Pupa* of de Monet de Lamarck, 1801, type species *Turbo uva* Linnaeus, 1758, by monotypy – synonym of *Cerion* Röding, 1798; Cerionidae. Not *Pupa* of Draparnaud, 1801, type species *Pupa secale* Draparnaud, 1801, by monotypy – synonym of *Abida* Turton, 1831; Chondrinidae.)

Zonites of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix algira* Linnaeus, 1758, by original designation; Zonitidae.)

Isthmia Gray, 1821: 239 (as a subgenus of *Helix* Linnaeus), type species *Helix (Isthmia) cylindrica* Gray, 1821 = *Vertigo pygmaea* (Draparnaud, 1801), by original designation.

Alaea Jeffreys, 1830: 357, type species *Alaea palustris* Leach, in Turton, 1831 = *Vertigo antivertigo* (Draparnaud, 1801), selected by Gray (1847).

Staurodon Lowe, 1855: 214 (as a subgenus of *Pupa*), type *Pupa pygmaea* Draparnaud, 1801, by original designation. (Not *Staurodon* of Lowe, 1852, type species *Pupa saxicola* Lowe, 1852, designated by Pilsbry (1918–20); Vertiginidae.)

Dexiogira Stabile, 1864: 104, type species *Pupa antivertigo* Draparnaud, 1801, designated by Franzen & Leonard (1947).

Haplopupa Pilsbry, 1898: 119 (as a section of *Vertigo* Müller), type species *Vertigo dalliana* Sterki, 1890, by monotypy.

Diagnosis. As for the subfamily (see above).

Remarks. Zilch (1959–60) recognised five subgenera of *Vertigo*, characterised by the apertural barriers and general shape of the shell: *Alloptyx* Pilsbry, 1953; *Angustula* Sterki, 1888; *Vertilla* Moquin-Tandon, 1855; *Vertillaria* Pilsbry, 1919; and *Vertigo* s.s. As proposed by earlier authors (e.g., Kennard & Woodward 1926), Zilch reduced many early subdivisions of the genus to synonymy with *Vertigo* s. str. This approach was followed by Schileyko (1984), except that he recognised *Isthmia* Gray, 1821 as being subgenerically distinct from *Vertigo* s.s. Following Taylor (1960), Bequaert & Miller (1973) reduced *Angustula* to a junior synonym of *Vertigo* s.s. In a detailed study of the *Vertigo* of Poland, Pokryszko (1990a) could find no anatomical characters supporting recognition of *Vertilla* as a separate subgenus. This finding lends weight to the suspicion that current subgeneric division in *Vertigo* is a matter of taxonomic convenience, with no phylogenetic basis. The sole species established in New Zealand, *V. ovata* (Say, 1822), has shell characters consistent with the current definition of *Vertigo* s.s., and subgeneric divisions of *Vertigo* are not recognised here.

Vertigo is represented in North America by about 60 species, in Eurasia by about 30 species, and in Africa by 3–5 species.

Vertigo ovata (Say)

Figures 59, 91, 131, 132, 161, 187, 239, 254, C27, M24, M25; Map 24

pygmaea of authors (not of Draparnaud, 1801).
ovata Say, 1822: 375 (*Pupa*).
antiquorum Cockerell, 1891b: 18 (as form of *ovata* Say) (*Pupa*).
diaboli Pilsbry, 1919 (1918–20): 88 (as subsp. of *ovata* Say) (*Vertigo*).
mariposa Pilsbry, 1919 (1918–20): 88 (as subsp. of *ovata* Say) (*Vertigo*).
hibbardi Baker, 1938: 126 (*Vertigo*).
teskeyae Hubricht, 1961: 62 (*Vertigo*).

Shell (Fig. 59) dextral, ovate, from very short and broad to strongly elongate, perforate, up to 1.8–2.7 mm high by 1.2–1.7 mm in diameter, of 4.5–5.5 rounded whorls with deep sutures, glossy to almost matt yellowish brown to chestnut, with sculpture of fine growth lines. Protoconch (Fig. M24) of approximately 1.2 whorls, smooth in appearance but with fine, irregular reticulate sculpture under high magnification. Aperture (Fig. M25) nearly semicircular, in adults with margin continuous, white and slightly thickened, reflected in all but upper palatal section, internally with 4–6 white barriers; outer margin usually bent inwards slightly and bearing an auricle. Parietal wall with a prominent medial barrier. Columella with a prominent perpendicular fold or knob; base often with a small, knoblike barrier set somewhat deeper than other barriers. Palatal wall with 2 high medial lamellae extending about 0.2 of a whorl in depth; upper palatal wall often with a vestigial barrier. Upper body wall with external palatal crest a little behind aperture margin. Umbilicus open and deep but extremely narrow, rarely closed.

Animal with sides of foot, mantle collar, and sole pale grey and head, tentacles, and dorsal part of foot steel blue-grey. Tail moderately long, extending to level of shell apex in active animal.

Reproductive system, Fig. 91. Ovotestis grey, comprising 2 lobes each of 4–6 pear-shaped acini embedded in digestive gland. Hermaphrodite duct relatively short, proximally slender and not convoluted, medially distended and mildly contorted, then abruptly narrowing to form a U-shaped talon on ventral surface of the large, linguiform albumen gland. Female pallial gonoduct sacculate, thick-walled. Free oviduct long, narrowing to insertion of bursa copulatrix duct. Bursa copulatrix sac-like, elongate, appressed against lateral aspect of proximal spermoviduct, on a slender, long duct. Vagina very short, stout. Prostatic gland comprising 2–4 elongate acini, often partially fused, opening over a very short length of male pallial gonoduct. Prostatic gland fused with female tract to form a short spermoviduct. Free vas deferens slender, inserted in proxi-

mal apex of epiphallus adjacent to insertion of phallic retractor muscle. Epiphallus slender, widest proximally and narrowing gradually to insertion into phallus. Phallus elongate, about 2x length and width of epiphallus, distinctly dilated at entry of epiphallus, internally with a small conical vergic papilla and low longitudinal folds. Atrium short.

Spermatophores unknown, apparently not produced.

Phallus retractor arising from diaphragm, running to insertion on epiphallus as a single muscle strand.

Jaw (Fig. 131) 0.12 mm wide, strongly arched, comprising 13 or 14 fused plates, each finely striate.

Radula (Fig. 132) with about 86 transverse rows of teeth, each varying in formula around 20 or 21 + C + 20 or 21. Central tooth well developed, tricuspid, with a large mesocone flanked on either side by a minute accessory cusp and a large ectocone, on a large rectangular basal plate. First lateral teeth similar to the central, but mesocone shortened to same length as ectocone and endocone. Laterals grading into marginals by gradual reduction in length of primary cusps, division of minute accessory cusps, and shortening of basal plate. Teeth on extreme margin of radular ribbon serrate.

Digestive tract, Fig. 161. Buccal mass spheroidal. Oesophagus long, slender, not differentiated into a crop. Gastric pouch cylindrical, extending about 0.5 of a whorl to merge with stomach, which is not externally differentiated. Intestine producing one forward loop and one posteriorly directed loop before running as rectum to anus in mantle collar.

Pallial complex, Fig. 187. Pulmonary cavity extending about 0.8 of body whorl, lacking all vascularisation but the primary vein. Kidney short, about as long as pericardium, sacculate, extending to about 0.8 of pulmonary cavity length by an elongate ureteric pouch, with excretory orifice laterally near anterior extremity. Closed retrograde ureter lacking, but a very short gutter directed towards lung top.

Free muscle system, Fig. 213. Columellar muscle dividing at origin into left and right branches. Left branch giving rise to stout buccal retractor before anteriorly dividing into ocular peduncle retractors and labial retractors. Right branch giving rise to tentacular and labial retractors before ramifying into a broad tail fan; branch to ocular peduncle crossing over phallus.

Central nervous system, Fig. 239. Cerebral commissure length about equal to cerebral ganglion width. Cerebropedal connectives slightly longer than cerebral ganglion width, the right connective slightly shorter than the left. Pleural ganglia markedly closer to cerebral ganglia than to pedal ganglia. Parietal ganglia sited medially between pleural and visceral ganglia. Visceral ganglion slightly to

right of median plane, owing primarily to shortness of right cerebropleural connective.

Haploid chromosome numbers unknown.

Type material. Philadelphia, Pennsylvania was selected as type locality by Pilsbry (1918–20).

Distribution. *V. ovata* is widely distributed in its native North America, from Alaska and northern Canada southwards over most of the U.S.A. to Florida, the Gulf of Mexico, the Mexican border, and California. The only known naturalised occurrence outside of North America is New Zealand.

Recommended common name. Grassland whorl snail.

Material examined. New Zealand. ND. Kaitaia, Dec 1986, in pasture. Waipu Caves, 9 Sep 1984, B.F. Hazelwood (MONZ M80208). Whangarei, Tikipunga, 26 Oct 1991, A.M. Spurgeon. Tokatoka, Jan 1982, P.C. Mayhill. **AK.** Wenderholm beach, 29 Dec 1986, B.F. Hazelwood & H. Taylor. Northcote, 23 Oct 1978, B.F. Hazelwood. **CL.** Coromandel, Sep 1991, H. Bland. **WO.** Port Waikato, Sep 1991. Waikaretu, 17 Sep 1977 and 11 Dec 1977, B.F. Hazelwood, limestone ledges (MONZ M57339, M58269, M68552). Maungakawa, Aug 1979 and Aug 1985, P.C. Mayhill. Whatawhata, Jan 1993, in limestone outcrops in pasture. Raglan, Waimai Valley, 1970–72, Hamilton Junior Naturalists Club (MONZ M45990). Te Aku, May 1977, P.C. Mayhill. Kiritehere, Apr 1980, P.C. Mayhill. **BP.** Motu River mouth, May 1980, P.C. Mayhill. **WI.** Wanganui, Virginia Lake, 12 Aug 1987 (MONZ M89809). **GB.** East Cape, Te Araroa, 29 Dec 1979, D.J. Roscoe (MONZ M70678).

History in New Zealand. Barker (1982) stated that in the early 1980s *V. ovata* was unknown outside the Auckland region, basing this on records of *Vertigo pygmaea* (Draparnaud, 1801) from Auckland by Willan (1977) (see Remarks for identity of New Zealand *V. pygmaea*). However, *Vertigo* was first recorded in New Zealand by Whitten (1955) for a single shell collected from McGregor's Bay, Whangarei in 1955. In addition, Mannering (1971) had reported on material from the Port Waikato area, Gardner (1977) from McGregor's Bay (Whangarei Heads), Pungaru (Hokianga Harbour), Waikaretu, and Te Akau, and Furey (1982) recorded *Vertigo* during an archaeological study at Whangapoua State Forest, Coromandel. Material examined in the course of the present study confirmed *V. ovata* to be widely distributed in the North Island, and to have been present outside the Auckland area before 1982.

Biology. Little information is available on the biology of *Vertigo* in New Zealand. All known populations are from pasture, grassy areas adjacent to forest, or grassy ledges on partially deforested limestone outcrops. *V. ovata* is widely distributed and known from a variety of habitats in North America, including woodland and grassland. According to Franzen & Leonard (1947), in Kansas *V. ovata* lives only in moist environs afforded by shaded slopes near streams and shores of ponds. Similarly, Bequaert & Miller (1973) indicated that *V. ovata* in the arid southwest U.S.A. often lives in muddy litter and on damp logs or semiaquatic plants, close to the edge of ponds and shallow creeks. The available data on European *Vertigo* (e.g., Shileyko 1984, Waldén 1969, 1971, 1986, Zeissler 1960, Pokryszko 1990a) suggests that the most widely distributed species exhibit regional preferences in habitat, particularly at the limits of their range.

Aspects of the reproductive biology of *Vertigo* have been described by Watson (1923), Steenberg (1925), and Pokryszko (1987, 1990a, b). Both self-fertilisation and outcrossing, the latter involving either euphallic or euphallic/aphallic partners, have been reported for *Vertigo*. Observations on live New Zealand *V. ovata* have, to date, been confined to collections made in January 1993 from grassland near Whatawhata. Five individuals from this population have been dissected and were found to be sexually mature, with fully formed male genitalia. Mating (Fig. 254) was observed twice between snails from this population; on both occasions copulation involved reciprocal insemination via everted phallic structures. Further study is needed to determine if this population – and indeed *V. ovata* – is dominated or constituted solely by euphallic individuals.

Mating was apparently initiated by one snail following and eating the mucus trail of another. The trail-layer was approached and palpated with the ocular peduncles, and its shell was mounted. In the two matings observed, several attempts at shell mounting were required for the snail initiating courtship to establish a firm hold and proper orientation. This phase took some 35–45 minutes, during which the individual receiving the attention showed no apparent interest, continuing to move about and feed. Eversion of the phallus and its tactile play over the head region, accompanied by secretion of a viscous mucus, initiated a response in the mounted individual, with cessation of movement and eversion of its phallus. Reciprocal intromission quickly ensued. Copulation lasted for 7–11 minutes, after which the phalluses were quickly retracted, the upper snail dismounted the lower individual, and both snails moved off to resume feeding as retraction of the phallus was completed.

Eggs of *V. ovata* have not been observed in the field in New Zealand. In the laboratory eggs were deposited singly on moist filter paper and among grass leaf litter. These

eggs were slightly oval, with a greater diameter between 0.5 and 0.55 mm, translucent, and gelatinous, and had no trace of calcium carbonate crystals.

Remarks. This small vertiginid, noted in the Northland and Auckland regions in the 1950s to 1970s, was referred to *V. pygmaea* (Draparnaud, 1801) (Whitten 1955, Mannering 1971, Willan 1977, Gardner 1977). As noted by Barker (1982), comparisons with shell lots of *V. pygmaea* from Europe and *V. ovata* from North America – not of the type series – by Dr F.M. Climo (formerly MONZ) suggested that the New Zealand shells belong to the latter. Since 1982 further populations of *Vertigo* have been discovered in northern New Zealand. All New Zealand populations are characterised as follows. (1) A protoconch of rather flat apex and rapidly expanding whorl. (2) Moderately convex teleoconch whorls without spiral striate sculpture. (3) Aperture with 4–6 barriers, always with only one (medial) parietal lamella, one columellar lamella, and superior and inferior palatal plicae; when present, basal fold more subcolumellar than palatal. (4) Palatal plicae on an internal ridge associated with a more-or-less prominent crest on shell exterior. (5) Aperture margin slightly thickened, and reflected in columellar and basal regions. (6) Peristome continuous. (7) Outer margin of aperture with an auricle, but inward bend weakly developed. On these shell characters the New Zealand stock is intermediate between the *V. ovata* group *sensu* Pilsbry (1948 (1939–48)) and *V. pygmaea* in the sense of Pilsbry (1948 (1939–48)) and Pokryszko (1990a).

The aperture in juvenile New Zealand shells is square in outline, cf. circular in *V. pygmaea*. The anatomy of the reproductive system in the New Zealand material departs from *V. pygmaea* and other European *Vertigo* (see Steenberg 1925, Schileyko 1984, Pokryszko 1990a) in the following combination of character states: very elongate phallus, very short epiphallus, and distal insertion of bursa copulatrix duct. To my knowledge no North America *Vertigo* has been studied anatomically, including the North American forms of *V. pygmaea*, so that no definitive conclusion on affinities of the New Zealand stock can be drawn. Assignment of the New Zealand populations to *V. ovata* is tentatively retained, pending anatomical investigation of North American taxa.

The bipartite structure of the phallus referred to by Pokryszko (1990a, b) is here interpreted as comprising a proximal epiphallus and a distal phallus, with only the latter everted during copulation. This is consistent with Steenberg (1925) and Schileyko (1984).

An introduction into the literature on *V. ovata* is provided by Pilsbry (1922–26, 1948 (1939–48)), Fransen & Leonard (1947), and Bequaert & Miller (1973).

Family ZONITIDAE

Diagnosis. Herbivorous or carnivorous aulacopod snails able to withdraw completely into the shell. Shell generally thin, glossy and translucent, globulose to strongly depressed or discoidal, umbilicate or imperforate. Posterior caudal pit not overhung by a horn-like prominence. Mantle without prominent lobes reflexed over shell. Sole divided into longitudinal zones, or undivided. Suprapedal gland embedded in foot tissues. Buccal mass spheroidal (herbivores) to elongate (carnivores). Jaw oxygnathous, with a medial anterior projection. Radula with aculeate marginal teeth. Intestine with a single loop directed forwards. Kidney triangular, less than twice length of pericardium. Ureter sigmoid, closed to pneumostome. Central nervous system with cerebropedal connectives equal in length, or left connective the longer, 1.2–3x cerebral ganglion width. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact.

Haploid chromosome number 20–31.

Remarks. In the Zonitidae I recognise two subfamilies, Gastrodontinae and Zonitinae.

Subfamily ZONITINAE

Diagnosis. Shell minute to moderately large. Genital orifice located at some distance posterior to right ocular peduncle. Genitalia without a dart sac or epiphallic papilla. Bursa copulatrix duct without a diverticulum. Pleural ganglia close to pedal ganglia, on short but distinct pleural/pedal connectives. Visceral chain compact, often with some ganglia fused.

Haploid chromosome number 24–31.

Genus *Oxychilus* Fitzinger

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Zonites of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix algira* Linnaeus, 1758, by original designation; Zonitidae.)

Oxychilus Fitzinger, 1833: 100, type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847) [ICZN Opinion 431, 1956: 350].

Vitrea of authors. (Not *Vitrea* of Fitzinger, 1833, type species *Glischrus* (*Helix*) *diaphana* Studer, 1820, by monotypy [ICZN Opinion 335, 1955a: 50, 59]; Zonitidae.)

Vortex of authors. (Not *Vortex* of Beck, 1837 (1837–38), listed in synonymy of *Helicodonta* d'Audebard de Férussac, 1819, Helicidae, by Zilch (1959–60), type designation not traced.)

Polita Held, 1838 (1837–38): 916, type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847).

Hyalina de Charpentier, 1837: 13 (as subgenus of *Helix* Linnaeus), type species *Helix lucida* Draparnaud, 1801, designated by Bourguignat (1890). (Not *Hyalina* of Studer, 1820, listed in synonymy of *Vitrina* Draparnaud, 1801, Vitrinidae, by Zilch (1959–60), type designation not traced. Not *Hyalina* of Schumacher, 1817, type species *Hyalina pellucida* Schumacher, 1817, by monotypy; Gastropoda, Marginellidae. Not *Hyalina* Rambur, 1866; Lepidoptera.)

Helicella Gray, 1847: 173, type species *Helix cellaria* Müller, 1774, by original designation. (Not *Helicella* of d'Audebard de Férussac, 1821, type species *Helix ericetorum* Müller, 1774 = *Helicella itala* (Linnaeus, 1758), designated by Herrmannsen (1847) [ICZN Opinion 431, 1956: 350]; Hygromiidae.)

Amphidoxa of authors. (Not *Amphidoxa* of Albers, 1850, type species *Helix marmorella* Pfeiffer, 1845, designated by Pilsbry (1893–95 (1890–95)); Endodontidae.)

Hyalinia Albers, 1850: 66 (as group in *Helix* Linnaeus), type species *Helix cellaria* Müller, 1774, designated by von Martens (1860).

Lucilla Lowe, 1855: 177, type species *Helix cellaria* Müller, 1774, by original designation.

Aplostoma Moquin-Tandon, 1855: 72 (as section of *Zonites* de Montfort), type species *Helix cellaria* Müller, 1774, designated by Lindholm (1927).

Euhyalina Albers, 1857: 91 (as group of *Hyalinia* de Charpentier, 1837), type species *Helix cellaria* Müller, 1774, by original designation.

Zonitoides of authors. (Not *Zonitoides* of Lehmann, 1862, type species *Helix nitida* Müller, 1774, by monotypy [ICZN Opinion 335, 1955a: 50, 59]; Zonitidae.)

Flammulina of authors. (Not *Flammulina* of von Martens, 1873, type species *Vitrina zebra* Le Guillou, 1842, according to Pilsbry (1893–95 (1890–95)); Charopidae.)

Gerontia of authors. (Not *Gerontia* of Hutton, 1882a, type species *Gerontia pantherina* Hutton, 1882a, by monotypy; Charopidae.)

Calymna of authors. (Not *Calymna* of Hutton, 1884, type species *Amphidoxa costulata* Hutton, 1882, by monotypy – synonym of *Flammulina* von Marten, 1873; Charopidae.)

Euhyalinia Taylor, 1907 (1906–14 (1902–21)): 18 (as subgenus of *Hyalina* de Charpentier), emended name for *Euhyalina* Albers, 1857.

Diagnosis. Essentially vegetarian species, but with a tendency to predaceous feeding on snails and slugs. Shell small to medium-sized (diameter to 30 mm), thin, strongly depressed, with spire only slightly raised, umbilicate, with 4–7 rounded, gradually to rapidly expanding whorls; aperture rounded to elliptical; lip thin, with no internal callus or barriers. Animal with glandular phylacites and pits in right anterior skin. Foot long and narrow, with distinct pedal grooves and posterior caudal mucus pit; sole tripartite, in progression showing distinct waves over central area. Buccal mass tending to elongate. Jaw arched,

smooth, with a central projection. Radula with marginal teeth elongate, aculeate. Intestine with a single loop directed forwards. Kidney triangular, not much longer than pericardium. Ureter sigmoid, its secondary part closed to pneumostome. Genital orifice approximately midway between pneumostome and right ocular peduncle. Genitalia characterised by a proximal vaginal gland, an epiphallic tube sometimes with a small flagellum, entering phallus apically or subapically, and a muscular sheath about distal part of phallus, the latter typically enclosing terminal part of vas deferens. Bursa copulatrix duct simple, never long. Right ocular retractor passing between phallus and vagina.

Haploid chromosome number 24–30.

Remarks. The genus *Oxychilus*, represented by in excess of 100 species, occurs throughout Europe. The uniformity in shell form is remarkable, and reliable identifications are dependent on study of anatomy.

On the basis of characters of the shell, radula, and genitalia, Forcart (1957) and Riedel (1980) recognised respectively 8 and 22 subgenera of *Oxychilus*. Of relevance to the species established in New Zealand, both of them classified *O. draparnaudi* (Beck, 1837) in subgenus *Oxychilus* s.s., along with the type species *O. cellarius* (Müller, 1774), while *O. alliarius* (Miller, 1822) was classified in subgenus *Ortizius* Forcart, 1957, typified by *O. helvetica* (Blum, 1881). In support of earlier observations (Manganelli & Giusti 1985, Altonaga 1986, Manganelli *et al.* 1991), de Brito (1992) has shown *Ortizius* to be a junior synonym of *Oxychilus* s.s.

The four *Oxychilus* species represented in Britain have been widely distributed through the trading activities of man. Three of these have established in New Zealand. The keys developed by Lloyd (1970b, c) for separation of the British *Oxychilus*, based on glandular features of the anterior body wall, can – in conjunction with shell characters – be usefully employed for identification of New Zealand material when live specimens are available but anatomical dissections are not practicable.

Subgenus *Oxychilus* Fitzinger

Oxychilus Fitzinger, 1833: 100, type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847).

Mediterranea Clessin, 1880b: 207 (as group of *Hyalinia* de Charpentier, group *Vitrea* Fitzinger), type species *Helix hydatina* Rossmässler, 1838, by original designation.

Hydatina Westerlund, 1886 (1886–87): 29, 37 (as section of *Hyalinia* Charpentier, group *Vitrea* Fitzinger), type species *Helix hydatina* Rossmaessler, 1838, by monotypy. (Not *Hydatina* of Ehrenberger, 1828; Rotatoria.)

Hyalofulgida di Maria di Monterosato, 1892: 7 (as group of

Hyalinia Westerlund), type species *Helix villae* Mortillet *in* Strobel, 1853 (not of Deshayes, 1850) = *Helix mortilleti* "Stabile" Pfeiffer, 1859, designated by Riedel (1973).

Retinella sensu Westerlund, 1902: 86, type species *Helix fuscosa* Rossmässler, 1838, by original designation. (Not *Retinella* of Fischer *in* Shuttleworth, 1877, type species *Helix olivetorum* Gmelin, 1791, designated by Kobelt (1880 (1876–81)); Zonitidae.)

Hydatinus Wagner, 1907: 108, as amended name for *Hydatina* Westerlund, 1886.

Diaphanella Hesse, 1916: 124, new name for *Hydatina* Westerlund, 1886. (Not *Diaphanella* of Clessin, 1880b, type species *Glischrus* (*Helix*) *diaphana* Studer, 1820, by original designation – synonym of *Vitrea* Fitzinger, 1833; Zonitidae. Not *Diaphanella* of Thiele, 1912, type species *Bulla fragilis* Vélain – synonym of *Notodiaphana* Thiele, 1917; Gastropoda, Diaphanidae.)

Geodiaphana Thiele, 1917: 23, new name for *Hydatina* Westerlund, 1886 and *Diaphanella* Hesse, 1916.

Retinella sensu Lindholm, 1927: 323, type species *Helix fuscosa* Rossmaessler, 1838, by original designation. (Not *Retinella* of Fischer *in* Shuttleworth, 1877, type species *Helix olivetorum* Gmelin, 1791, designated by Kobelt (1880 (1876–81)); Zonitidae.)

Lindholmella Boettger, 1930: 580, type species *Helix fuscosa* Rossmaessler, 1838, by original designation; new name for *Retinella* sensu Lindholm, 1927.

Ortizius Forcart, 1957: 125 (as subgenus of *Oxychilus*), type species *Hyalina* (*Polita*) *helvetica* Blum, 1881, by original designation.

Diagnosis. Central tooth tricuspid, narrow and generally shorter than adjacent lateral teeth. Vaginal gland enclosing basal part of spermathecal duct. Epiphallus opening subterminally into phallus.

Oxychilus (*Oxychilus*) *alliarius* (Miller)

Figures 60, 63, 92, 106, 133, 162, 188, 214, 240, C28, M26, M102, M103, M121, M122; Map 25

nitidus of authors (not of Müller, 1774).
nitens of authors (not of Gmelin, 1791).
alliaria Miller, 1822: 379 (*Helix*).
foetida Brown, 1827: figs 48, 52 (*Helix*).
remota Benson, 1851: 263 (*Helix*).
steenstrupii Mörch, 1857b: 75 (*Helicella*).
tasmanicus McLauchlan, 1954: 40 (*Oxychilus*).

Shell (Fig. 60) up to 3.5 mm high by 7 mm in diameter, strongly depressed, convex above, flattened below, of 4–4.5 rather rapidly expanding whorls, with suture moderately distinct. Coloration translucent pale yellowish brown to brown above, paler around umbilicus below, glossy, with weak, rather regular striations. Protoconch (Fig. M26) smooth. Umbilicus about 0.17 of shell diameter.

Aperture slightly elliptical. Columella not reflected. Peristome thin.

Animal (Fig. 63) slate blue-black dorsally paling to grey at sides of foot; mantle collar grey; sole uniformly grey. Tail short, extending only a little beyond shell during locomotion. Locomotion by muscular pedal waves generated from posterior of sole. Mucus colourless. Phylacites well developed, densely clustered in body wall immediately anterior to mantle collar. Glandular crypts in anterior body wall few and inconspicuous, confined to right side.

Reproductive system, Fig. 92. Ovotestis whitish, composed of a few clusters of acini scattered amongst lobes of digestive gland. Hermaphrodite duct long, slender, not convoluted, medially distended, ending in a talon partially embedded in basal portion of large, linguiform albumen gland. Spermoviduct multilobate, slender proximally but rather voluminous distally, narrowing abruptly to free oviduct. Vagina stout. Vaginal gland enclosing basal part of bursa copulatrix duct and vagina, extending almost to genital atrium. Bursa copulatrix reservoir elongate oval to globulose, on a slender duct that broadens towards its insertion on oviduct. Vas deferens slender, arising at distal end of spermoviduct prostatic portion, united with epiphallus amongst muscle fibres of phallus sheath. Epiphallus slender, inserted subapically in phallus. Phallus elongate, cylindrical, with a poorly defined medial constriction below which it is enclosed by a thin muscular sheath, extending above insertion of epiphallus as a flagellum about 0.25 of length of phallus, internally the flagellum and region around epiphallus entry with slender pleats, and the distal phallus with papillate longitudinal folds. Atrium short.

Spermatophore (Fig. 106) a slender rod about 2.5 mm long, variably curved but always narrowed and pointed at ends, lacking elaborate external sculpture but with fine longitudinal striations.

Phallus retractor arising from diaphragm, inserted at apex of phallus flagellum.

Jaw (Fig. 133) about 0.5 mm wide, with a prominent medial projection.

Radular ribbon (Fig. M102, 103) with about 35 transverse rows of rather large teeth, each with a formula varying around 9–12+1+2+C+2+1+9–12. Central tooth similar in size to first lateral tooth, tricuspid, with mesocone slender but prominent and ectocones rather weak. First 2 lateral teeth with mesocone and endocones prominent, and ectocone weak; 3rd tooth transitional, with mesocone and endocone but lacking ectocone. Marginal teeth aculeate, unicuspid, decreasing in size rapidly towards radular margin.

Digestive tract, Fig. 162. Buccal mass longer than broad. Oesophagus abruptly widening into a bulbous crop,

then briefly narrowing before producing a voluminous gastric pouch that extends approximately half a whorl. Ducts of digestive gland inserted on stomach at distal extremity of gastric pouch; typhlosoles arising from digestive gland ducts and running side by side for several millimetres into intestine. Intestine arising from stomach, producing an anteriorly directed loop which abuts posterior wall of kidney, then passing posteriorly a short distance before running forwards to mantle margin as a rather voluminous rectal duct.

Pallial complex, Fig. 188. Pulmonary cavity extending to about 0.35 of body whorl in active animal, thus about 2x longer than broad. Venation of mantle roof distinct but not strongly developed. Kidney triangular, with pericardium extending along left side. Ureter a sigmoid, closed tube arising near anterior apex of kidney extending to top of pulmonary cavity along right side of kidney, and then fowards against rectum to pneumostome.

Free muscle system, Fig. 214. Cephalic retractors, comprising buccal, left tentacular, and right tentacular stems, arising separately from very near origin of columellar muscle. Ocular retractors branching at approximately midway to run to ocular peduncle and inferior tentacle. Buccal retractor bifurcating before its insertion on buccal mass. Main columellar branch a short, broad muscular fan penetrating lateral and pedal tissues of foot.

Central nervous system, Fig. 240. Cerebral ganglia united by a very short but distinct commissure. Left cerebropedal connective slightly longer than the right, its length about 1.2x width of cerebral ganglion. Pleural ganglia close to pedal ganglia, to which they are united by short connectives; right pleural ganglion appressed to right parietal ganglion; left pleural ganglion united to left parietal by a short connective. Visceral ganglion to right of median plane, closely appressed to right parietal ganglion but separated from left parietal by a short connective.

Haploid chromosome number 30.

Type material. The type specimens originate from the environs of Bristol, England, and are presumed to be lost.

Distribution. Widely distributed as a native in northern and western Europe. Introduced into Greenland, North America, St Helena, South Africa, Juan Fernandez, Australia, and New Zealand.

Recommended common name. Garlic glass snail.

Material examined. New Zealand. ND. Whangarei, 5 Aug 1977, in pasture. Mangawhai, Aug 1993, R. Parrish. AK. Goat I. Bay, Leigh, 5 Dec 1979, B.F. Hazelwood, under timber adjacent to build-ings. Dome Valley, 20 Apr 1987, B.F. Hazelwood & H. Taylor, in grassy area adjacent to Hotea River. Otakinini, 20 Oct 1978, in pasture. Kaukapakapa, 4 Mar 1976. Birkenhead, 1 Jan 1988, B.F. Hazelwood. Grafton, 31 Dec 1978, B.F. Hazelwood, in park garden. Mt Wellington, 20 Jun 1987, B.F. Hazelwood. Wiri, 19 Jan 1987, B.F. Hazelwood. CL. Little Barrier I., Aug 1983, P.C. Mayhill. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. WO. Komakorau, 18 Jul 1977, in grassy area at roadside. Matangi, 18 Apr 1979, under *Berberis* hedge. Hamilton, 6 Jan 1978, in garden. Rukuhia, 8 Jan 1977, in pasture at margin of peat lake. Cambridge, May 1990, in park greenhouse. Horo Horo, 2 Jul 1977, in park. Ohaupo, 13 Sep 1980, in gardens and greenhouses. Raglan, 16 Jul 1977, in grassy area at roadside. Te Uku, 16 Jul 1977, under rocks in pasture. Te Mata, 16 Jul 1977, in pasture. Kiritehere, Apr 1980, P.C. Mayhill. Waitomo, 19 Sep 1978, under rocks of limestone outcrop in pasture. Te Kuiti, 21 Sep 1978, in gardens. BP. Waihi Beach, 16 Jan 1994, in dunes under *Muehlenbeckia*. Tauranga, Aug 1988, in gardens. Papa-moa, Sep 1989, in exotic grasses in dunes. Lower Kaimai, 3 Mar 1988, in garden. GB. Wairoa, 22 Sep 1991, G. Foreman. TK. Manaia, 12 Aug 1983, F.F. Sideback. Hawera, 23 May 1979, L.T. Jones. WI. Foxton, 6 Dec 1980, in pasture. WN. Levin, 24 Apr 1980, G.S. Smith, in gardens. NN. Motueka, 6 Oct 1994, in grass on coastal bank. Cable Bay, 6 Oct 1994, in grass behind gravel beach. MC. Christchurch, 3 Oct 1991, A.D. Mannering, in garden.

Extralimital. England. Malham, Yorkshire, 1978, coll. & det. R.A.D. Cameron. Liverpool, Merseyside, 1977, coll. & det. N. McMillan. Little Witcombe, Gloucestershire, 21 Sep 1990, in oak woodland. Dorchester, Oxfordshire, 1 Dec 1990, in grassy area at roadside. Woodhenge, Wiltshire, 13 May 1990, in grassland. Queen Wood, Chiltern Hills, 16 Apr 1990. Kew Gardens, London, 9 Sep 1990, in greenhouses. **Netherlands.** Haarlem, Oct 1990, in grassy area at roadside. **Scotland.** Auchincruive, Dumfries & Galloway, 12 Sep 1990, in garden.

History in New Zealand. Musson (1891) recorded *Zonites nitidus* Müller, 1774 (= *Zonitoides nitidus*) from New South Wales, Australia, and Auckland, New Zealand. In the present study its occurrence here could not be confirmed, and it appears that the New Zealand records of Musson should be referred to *O. alliarius*, as was done by Taylor (1906–14 (1902–21)). Barker (1982) recognised the error in Musson's identification but wrongly listed this record under *O. cellarius* (Müller, 1774). Both *O. alliarius* and *Z. nitidus* occur in Australia, and it is therefore highly probable that Musson's records of *Z. nitidus* from that country encompass both species.

The records of Musson (1891) and Taylor (1906–14 (1902–21)) indicate that *O. alliarius* was well established in the North Island by the early twentieth century. Suter (1913) indicated that it was to be found in conservatories and hothouses.

Biology. In its native range *O. alliarius* lives in forest and open habitats, among leaf litter and under stones. Chat-

field (1975), for example, lists this species as a characteristic element of both grasslands and woodlands in Jersey. It also has been reported as a troglophile species (e.g., Evans & Jones 1973). In New Zealand *O. alliarius* occurs in a variety of modified habitats, including greenhouses, gardens, roadsides, hedgerows, parks, plantations, and pastures.

O. alliarius is primarily vegetarian, and gregarious. Frequently it attains pest status in greenhouses on tender plants such as ferns, and often occurs together with *Zonitoides arboreus*, which also damages plants. *O. alliarius* is also predatory on snails and snail eggs.

When disturbed *O. alliarius* liberates from gland cells in the mantle near the pneumostome an odour indistinguishable from that of garlic, hence the specific name (Latin: *allium* = garlic) and the vernacular name garlic snail. Lloyd (1969, 1970a, b) identified the principal volatile in the secretion as propyl mercaptan. In experiments using hedgehogs as predators, Lloyd showed that *O. alliarius* was rejected but other *Oxychilus* species, which do not produce the odour, were readily consumed. These results support the widely held opinion that the odour is a defensive adaptation produced on irritation.

The eggs are about 1 mm in diameter and white, owing to a calcareous shell (Fig. M121, 122).

Remarks. Taylor (1906–14 (1902–21)) illustrated and described a serrated ectocone on the lateral teeth of specimens of *O. alliarius* from Britain. In New Zealand material this cusp is not serrate, which is consistent with descriptions of *O. alliarius* from, for example, Australia (Laws 1966) and Spain (Castillejo 1985).

Entry into the literature on *O. alliarius* is provided by Germain (1930), Pilsbry (1946 (1939–48)), Likharev & Rammel'meier (1952), Giusti (1969), and Castillejo (1985).

Oxychilus (Oxychilus) cellarius (Müller)

Figures 61, 64, 93, 107, 134, 215, 241, C29, M27, M28, M104, M105, M123, M124; Map 26

cellaria Müller, 1774: 28 (*Helix*).
lucidus of authors (not of Draparnaud, 1801).
nitidula of authors (not of Draparnaud, 1805).
nitens of authors (not of Michaud, 1831).
glaphyra Say, 1816: 8 (*Helix*).
corneo-fulva Pfeiffer, 1862: 148 (*Helix*).
sydneyensis Cox, 1864: 37 (*Helix*).
farinesianus Bourguignat, 1870 (1863–70): 11 (*Zonites*).
navarricus Bourguignat, 1870 (1863–70): 13 (*Zonites*).
chersa Bourguignat, 1877: 38 (*Hyalinia*).
montsicci Fagot, 1890: 224 (*Hyalinia*).

neglecta Fagot, 1890: 225 (*Hyalinia*).
heracleensis Westerlund, 1893 (1892–94): 118 (*Hyalinia (Polita)*).
subfarinesiana Locard, 1894: 41 (*Hyalinia*).
lusitanica Locard, 1899: 17 (*Hyalinia*).
rouvieri Locard, 1899: 17 (*Hyalinia*).
lauta Locard, 1899: 23 (*Hyalinia*).
blidahensis Locard, 1899: 24 (*Hyalinia*).
hibernica Kennard, 1907: 327 (*Vitrea (Hyalinia)*).
scharffi Kennard, 1908: 50 (*Vitrea*).
pulchro-striatum MacMillan, 1940: 731 (*Oxychilus*).

Shell (Fig. 61) of mature snails about 5 mm high by 10 mm in diameter, occasionally to 14 mm, strongly depressed, convex above, flattened below, of 5–6 rather rapidly expanding whorls, with suture virtually flush. Coloration translucent horn brown or yellowish above, paler around umbilicus below, glossy, with faint irregular growth lines. Protoconch (Fig. M27, 28) of about 1.5 whorls, smooth. Umbilicus about 0.15 of shell diameter. Aperture elliptical. Columella not reflected. Peristome thin.

Animal (Fig. 64) blue-grey dorsally, fading to almost white at foot margins; sole pale; mantle edge grey, speckled and spotted grey and brown. Mucus thin, colourless. Tail protruding a short distance in crawling animal. Locomotion by muscular pedal waves generated from posterior of sole. Phylacites distributed over most of anterodorsal body wall, borne on tuberosities. Epithelial crypts absent from anterior body wall.

Reproductive system, Fig. 93. Ovotestis whitish, composed of acini closely clustered about origin of hermaphrodite duct and embedded amongst lobes of digestive gland. Hermaphrodite duct long, slender, not convoluted, medially distended, ending in a diverticulate talon partially embedded in basal portion of large, linguiform albumen gland. Spermoviduct multilobate, slender proximally but rather voluminous distally, narrowing abruptly to free oviduct; prostatic follicles weak or absent in proximal part, but strongly developed distally. Vagina stout; vaginal gland enclosing basal part of bursa copulatrix duct and vagina, extending almost to genital atrium. Bursa copulatrix reservoir elongate oval to globulose, on a slender duct that broadens towards its insertion on oviduct. Vas deferens slender, arising at distal end of spermoviduct prostatic portion, united with epiphallus amongst muscle fibres of phallus sheath. Epiphallus rather short, not twisted, inserted subapically on phallus, broad immediately after origin in vas deferens but becoming slender in distal part. Phallus elongate, cylindrical, with a poorly defined medial constriction below which it is enclosed by a thin muscular sheath, extending above insertion of epiphallus as a short flagellum about 0.15–0.18x length of phallus body, internally covered with rather large papillae, which

in flagellum and around epiphallus entry fuse to form a series of small pleats, and in distal section tend to coalesce as longitudinal folds. Atrium short.

Spermatophore (Fig. 107) about 3 mm long, in general shape as for *O. alliarius*.

Phallus retractor as in *O. alliarius*.

Jaw (Fig. 134) about 0.8 mm wide, of similar shape to that in *O. alliarius*.

Radular ribbon (Fig. M104, 105) with relatively few teeth, each of the formula 12+3+C+3+12. Central tooth tricuspid, narrower and shorter than lateral teeth, with mesocone shorter than basal plate, and ectocones very weak. Lateral teeth very large, conspicuously tricuspid. Marginal teeth thorn-shaped, without endocones or ectocones, the inner ones very large but diminishing in size rapidly towards edge of radula.

Digestive tract and pallial organs as for *O. alliarius*.

Free muscle system, Fig. 215. Cephalic retractors comprising buccal, left tentacular, and right tentacular stems, arising separately from dorsal aspect of broad tail fan, very near origin of columellar muscle. Ocular retractors branching anteriorly to run to ocular peduncles and inferior tentacles. Buccal retractor not markedly bifurcate before insertion on buccal mass.

Central nervous system, Fig. 241. Cerebral ganglia united by a very short but distinct commissure. Left cerebropedal connective longer than the right, its length about 1.5x width of cerebral ganglion. Pleural ganglia close to pedal ganglia, linked to pedal and parietal ganglia by short connectives. Visceral ganglion closely appressed to right parietal ganglion but separated from left parietal ganglion by a short connective, lying to right of median plane.

Haploid chromosome number 24.

Type material. Müller's type material, collected from wine cellars in Copenhagen, is presumed to be lost.

Distribution. Native to western and central Europe and the western Mediterranean. Introduced to Scandinavia, North America, South America, the Philippines, South Africa, St Helena, Australia, and New Zealand.

Recommended common name. Cellar glass snail.

Material examined. New Zealand. ND. Spirits Bay, 10 Aug 1977, S.S. Jones, in pasture. Taipa, 18 Sep 1971, F.M. Climo (MONZ M38216); 9 Oct 1976, B.F. Hazelwood (MONZ M55398). Mangonui, Oruru Valley, 1986, R. Wallace (MONZ M87656). Herekino Gorge, 4 Jan 1976, B.F. Hazelwood (MONZ M69179). Mangamuka, Otongaroa Cave, Nov 1984, coll. T. Worthy (MONZ M81742); Kaeo, Pupuke, M. Holloway & A.G. Stevenson (MONZ M84750). N Mangamuka Gorge, 30 Dec 1978, D.J. Roscoe (MONZ M61921). Motukaraka, Nov 1984, P.C. Mayhill (MONZ M82287). Waiare, Nov 1987, P.C. Mayhill (MONZ M97905). Opononi, Motutoa, 1989, C. Frederickson (MONZ M97503). Kerikeri, 14 Dec 1977, in gardens. Waipu Caves, Mar 1976, B. Penniket, 8 Jul 1978, 7 Aug 1978, and 9 Sep 1984, B.F. Hazelwood (MONZ M68408, M70537, M80205). Waima, Jan 1990, P.C. Mayhill. Maunganui Bluff, 6 Oct 1976, D.J. Roscoe (MONZ M61931). Tikipunga, 14 Sep 1977, under stones in park. Ngungura, May 1978, P.C. Mayhill. Bland Bay, 17 Dec 1989, B.F. Hazelwood & S. O'Shea. Whangaruru Bay, 17 Feb 1989, B.F. Hazelwood. Dargaville, Montgomery's Bush, Apr 1983, P.C. Mayhill (MONZ M82708). **AK.** Goat I. Bay, Leigh, 5 Dec 1979, B.F. Hazelwood, under *Phormium* on coastal cliffs. Leigh, 13 Feb 1977, in pasture. Mangakura, 20 Apr 1987, B.F. Hazelwood & H. Taylor; Hoteo, 20 Apr 1987, B.F. Hazelwood & H. Taylor, in grassy area adjacent to Hoteo River. Kaipara Flats, Thompson's Bush Scenic Reserve, 28 Sep 1983, B.F. Hazelwood (MONZ M75724). Warkworth, 1935, M. Holloway & A.G. Stevenson (MONZ M84652, M84833); 1 Jan 1976, B.F. Hazelwood (MONZ M69231). Warkworth, The Sandspit, 3 Mar 1985, B.F. Hazelwood (MONZ M76772). Kawau I., Oct 1983, P.C. Mayhill. Mahurangi Regional Park, 31 Jan 1987, B.F. Hazelwood. Waiwera, 29 Dec 1986, B.F. Hazelwood & H. Taylor (MONZ M97628). Wenderholm beach, 29 Dec 1986, B.F. Hazelwood & H. Taylor. Parakai, Nov 1980, P.C. Mayhill (MONZ M63257). Orewa, Eaves Reserve, 4 Jan 1987 and 20 Apr 1987, B.F. Hazelwood & H. Taylor (MONZ M97528, M99569). Silverdale, Dec 1938 (MONZ M84897). Muriwai, 1986, R. Wallace, in dunes (MONZ M87680). Hobsonville RNZAF, Dec 1980, P. Sudlow (MONZ M70749). Birkenhead, 1 Jan 1988, B.F. Hazelwood. Devonport, Sep 1920, W.R.B. Oliver (MONZ M13273). Grafton Valley, 25 Sep 1977, B.F. Hazelwood (MONZ M57313). Grafton Gully, Nov 1985, J.F. Goulstone. Auckland Domain, Aug 1986, J.F. Goulstone. Orakei, Kepa Reserve, Aug 1985, J.F. Goulstone, in forest remnant. Howick, Shelley Park, 2 Aug 1987, J.F. Goulstone, in scrubland. Titirangi, 29 Oct 1977, associated with potted plants in nursery. Blockhouse Bay, 4 Oct 1986, B.F. Hazelwood & H. Taylor (MONZ M99478). Cockle Bay, 17 Jan 1988, B.F. Hazelwood. Panmure, 26 Oct 1986, B.F. Hazelwood. Mangere, 25 Sep 1983, B.F. Hazelwood. Mt Eden, M. Holloway & A.G. Stevenson (MONZ M84653, M84761); 3 Mar 1987, B.F. Hazelwood. East Tamaki, Oct 1987 (MONZ M97447). Morningside, 1933 and 1935, M. Holloway & A.G. Stevenson (MONZ M84760, M84654). Mt Wellington, 20 Jun 1987, B.F. Hazelwood. Ellerslie, 12 Jul 1987, B.F. Hazelwood (MONZ M99493). Manurewa, Idesia Place Reserve, Oct 1987, J.F. Goulstone, in forest remnant. Howick, 2 Aug 1987, J.F. Goulstone, in forest remnant. Manukau, Murphy's Bush, Nov 1985, J.F. Goulstone, in forest remnant. Manukau, 17 Jan 1988, B.F. Hazelwood. Papatoetoe, Puhini, 1961, W. Ponder (MONZ M20575). Duder's Beach, 11 Mar 1990, J.F. Goulstone, in forest remnant. Ponga, 13 Jun 1987, J.F. Goulstone, in remnant forest. N Waiuku Beach, 14 Jan 1978, B.F. Hazelwood (MONZ M69268). Waiuku, Crispe's Bush, 16 Nov 1981, F.M. Climo & D.J. Roscoe (MONZ M77785). N Mercer, 24 Sep 1978, B.F. Hazelwood (MONZ M69245). Hunua Ranges, Cossey's Dam Track, Aug 1979, J.F. Goulstone, under *Blechnum* on roadside. Raventhorp, 13 Jul 1988, J.F. Goulstone, in forest remnant. Red

Hills, Puke Kiwiriki Pa, 7 Sep 1986, J.F. Goulstone, in forest remnant. Waitakaruru Scenic Reserve, Nov 1985, J.F. Goulstone, in forest litter. **CL**. Mayor I., 26 Jan 1978, K. Brown (MONZ M82431). Tokatea, May 1981, P.C. Mayhill. Flaxmill Bay, 20 Feb 1978, in coastal *Metrosideros excelsa* forest. Opoutere, 29 May 1996, coll. G.M. Barker & M.P. Barker, in coastal forest, 15 m alt. **WO**. Limestone Downs, 13 Feb 1981, N. Douglas (MONZ M77903). Waikaretu, 17 Sep 1977, B.F. Hazelwood (MONZ M57337); 11 Dec 1977, B.F. Hazelwood (MONZ M68531, M68531). Matamata, Crystal Springs, 26 Jan 1961, A.G. Beu (MONZ M32028). W Ngaruawahia, 20 Sep 1977, B.F. Hazelwood (MONZ M 57322). Hinuera, 8 Jan 1993, in *Podocarpus dacrydioides* forest remnant. Maungakawa, Aug 1979, P.C. Mayhill. Hamilton, 27 Aug 1977 and 11 Jul 1978, in pasture; 15 Oct 1977, B.F. Hazelwood (MONZ M68528); 29 Dec 1978, in garden. Rukuhia, 4 Mar 1976 and 15 May 1977, in pasture. Te Kowhai, 19 Sep 1978, in grassy area at roadside. Whatawhata, 12 Feb 1978, B.F. Hazelwood (MONZ M58274). Raglan, Waimai Valley, 11 Dec 1977, B.F. Hazelwood (MONZ M68551). Karamu, 1970–72, S. Easterbrook-Smith (MONZ M45670, M45819). Raglan, 16 Jul 1977, under rocks at roadside. Te Akau, Sep 1981, P.C. Mayhill. Karapiro, 19 Oct 1982, B.F. Hazelwood (MONZ M73957). Kihikihi, Owairaka Valley, B.F. Hazelwood (MONZ M97690). Kakepuku, 15 Jan 1977, under stones in pasture. Kawhia, Anderson's Bluff, 22 Oct 1977, B.F. Hazelwood (MONZ M57575). Kawhia Harbour Scenic Reserve, 15 Aug 1977, B.F. Hazelwood (MONZ M62621). Otewa, 19 Dec 1977, under *Eucalyptus* logs in pasture. E Maungapohue, 16 Oct 1977, B.F. Hazelwood (MONZ M57479). Maungapohue Natural Bridge, W Waitomo, 16 Oct 1977, B.F. Hazelwood (MONZ M57364). Waitomo, 7 Sep 1968, D.J. Roscoe (MONZ M89562); 4 Jan 1977, B.F. Hazelwood (MONZ M55160); 13 Nov 1977, B.F. Hazelwood (MONZ M68498); 8 Dec 1978, under rocks of limestone outcrop at forest edge. Waitomo, Ruakuri Caves, Jul 1977, P.C. Mayhill. Te Kuiti, Aug 1977 and 28 Mar 1977, in gardens. Oparure, 25 Oct 1977, under limestone rocks in pasture and at roadside. Te Kuiti, Mangaokewa Scenic Reserve, Nov 1980, P.C. Mayhill (MONZ M82236); 9 Apr 1978, B.F. Hazelwood (MONZ M81844). Paemako, undated, M. Holloway & A.G. Stevenson (MONZ M84850). Mahoenui Valley, 5 Mar 1977, F.M. Climo (MONZ M56844). **BP**. Karewa I., 29 Feb 1948, R.A. Falla (MONZ). Waihi Beach, 16 Jan 1994, in dunes and gardens. Bowentown Heads, 26 Dec 1973, N.J. Peterson (MONZ M82567). Otumoetai, 26 Dec 1988, B.F. Hazelwood. Whakamarama, May 1990, P.C. Mayhill. Tauranga Arch. Survey, 1984, B. McFadgen (MONZ M86057). Papamoa Beach, 9 Sep 1989 and 5 Jun 1991, in dunes under *Muehlenbeckia*. Ohope, Jan 1959, A.G. Beu (MONZ M32027). Ohiwa Harbour, Uretawa I., Jul 1984, G.M. Beadel (MONZ M79583). Cape Runaway, Waihau Bay, 8 Mar 1962, R.K. Dell (MONZ M22021). Hicks Bay, E Haupara Point, 19 May 1983, F.M. Climo (MONZ M78336). Lower Kaimai, 27 Dec 1977, in garden. Lake Okareka, Acacia Bay, 10 Dec 1977, B.F. Hazelwood (MONZ M68886). **GB**. East Cape, Te Araroa, 29 Dec 1979, D.J. Roscoe (MONZ M70677). Te Araroa, Dec 1980, P.C. Mayhill (MONZ M76696). East Cape, Pakuraiti, 19 May 1983, F.M. Climo (MONZ M78161). East Cape, Oct 1982, P.C. Mayhill (MONZ M76943); 19 May 1983, F.M. Climo (MONZ M77994); Jan 1985, L. Daniel (MONZ M76484). Hikurangi, 12

May 1983, F.M. Climo (MONZ M78098). Te Puia Springs, 11 May 1983, F.M. Climo (MONZ M78288). Tokomaru Bay, 16–19 May 1983, F.M. Climo (MONZ M78371, M78218). Puha, 18 Sep 1979, in pasture. Te Arai Scenic Reserve, Jun 1987, P.C. Mayhill (MONZ M99353). Pakarae, undated, N.J. Peterson (MONZ M82643). **TK**. Mokau, 5 Mar 1977, F.M. Climo (MONZ M56729). N Waitara, Feb 1984, B.F. Hazelwood (MONZ M79798). New Plymouth, 10 Mar 1977, F.M. Climo (MONZ M55936); 5 Feb 1984, B.F. Hazelwood (MONZ M79790). Mt Egmont, Dawson Falls, P.C. Mayhill. Hawera, 22 Oct 1972, D.J. Roscoe (MONZ M98916). **HB**. Tangoio Falls, P.C. Mayhill; 25 Feb 1968, D.J. Roscoe (MONZ M89494). Napier, Bluff Hill, Dec 1935, H.B. Fell (MONZ). Hastings, W. Ponder (MONZ M20443). Waipukurau, Hatuma, 30 Dec 1959, J.C. Yaldwyn (MONZ M15160). Wai-pukurau, Pukeora Hill, 8 Mar 1977, B.F. Hazelwood (MONZ M69860). **RI**. Ohakune, Ranger Station Track, Dec 1981, P.C. Mayhill. Ngamatapouri, 2 Apr 1972, D.J. Roscoe (MONZ M96841). **WI**. Waitotara, 3 Apr 1972, D.J. Roscoe (MONZ M98113). S Kai-iwi, 14 May 1977, B.F. Hazelwood (MONZ M56228). Wanganui, Virginia Lake, 29 Jul 1984 and 12 Aug 1987, B.F. Hazelwood (MONZ M75366, M89807). Wanganui, 13 Jun 1975, E.M. Andrews (MONZ M38710); 19 Oct 1975, D.J. Roscoe (MONZ M80825). Longacre, 10 Apr 1937, O'Connor (MONZ). **WN**. Otaki, 24 Dec 1979, B.F. & N.P. Hazelwood (MONZ M63085). Waikanae, W. Ponder (MONZ M20442); A.G. Beu (NMNZ M32115). Mana I., 1952, J.C. Yaldwyn (MONZ). Porirua, 1958, A.G. Beu (MONZ M32029). Wellington, Evans Bay, 2 Aug 1979, F.M. Climo (MONZ M77229). **NN**. Puponga, Abel Head, 28 Dec 1971, F.M. Climo (MONZ M37894); 28 Aug 1978 (MONZ M58062). Puponga Point, 17 Mar 1971, 13 Jan 1980, 9 Apr 1982, and 17 Jan 1987, F.M. Climo (MONZ M63019, M38189, M70426, M86376). N Fossil Point, 7 Jan 1980, F.M. Climo (MONZ M63045). Parapara Spit, Aug 1977, B. McFadgen (MONZ M58104). Rockville, Devils Boots, undated, P.R. Jamieson (MONZ M88836). Takaka, Copperstain Ck, 11 Mar 1976, D.J. Roscoe (MONZ M56891). Takaka, Jan 1973, B.F. Hazelwood (MONZ M76760). Paturau, 17 Mar 1955, R. Ordish (MONZ M14538). Nelson, 11 Oct 1935, W.R. Arthur, M. Holloway, & A.G. Stevenson (MONZ M84907). **BR**. Punakaiki, 27 Apr 1983, P.R. Millener (MONZ M77852, M77903, M78460). Paparoa, 5 Oct 1976, B.F. Hazelwood (MONZ M69800). Paparoa N.P., Bullock Creek, Jan 1987, P.C. Mayhill (MONZ M96763). Greymouth, Point Elizabeth Walkway, Jan 1987, P.C. Mayhill (MONZ M96781). Greymouth, Jan 1988, P.C. Mayhill (MONZ M98779). Moana, 10 Mar 1950, R.R. Forster (MONZ M28991). **MC**. Christchurch, Rolleston, Jun 1979, MAF (MONZ M75399). **WD**. Franz Josef Village, 11 Jan 1982, G. McSweeney (MONZ M73757). Jackson Bay, 6 Jul 1969, J.C. Yaldwyn (MONZ M37728). **SC**. Timaru, 24 May 1992, J.S. Clarke. **DN**. Dunedin, 7 Jan 1988, A. Harris, in gardens.

Extralimital. England. Liverpool, Merseyside, 1977, coll. & det. N. McMillan. Little Witcombe, Gloucestershire, 21 Sep 1990, in oak woodland. Lashford Lane Fen Reserve, Oxfordshire, 22 Sep 1990, under stones in grass area. Dorchester, Oxfordshire, 1 Dec 1990, in churchyard. Maidenhead Thicket, Berkshire, 28 Apr 1990, under stones and twigs. **Ireland**. Glenarm, Antrim, 30 Aug 1990, in coastal limestone cliffs. **Netherlands**. Uithoorn, 23 Oct 1990, in grass on canal bank.

History in New Zealand. *O. cellarius* was first recorded in New Zealand by Pfeiffer (1862), who described it as a new species, *Helix corneo-fulva*. Pfeiffer's species, collected from the Bay of Islands, was considered to be an element of the indigenous fauna by several New Zealand malacologists (e.g., Suter 1891, 1893a, Crosse 1893, Hedley & Suter 1893, Suter 1894) although Hutton (1883), Tryon (1886) and later Suter (1904) reduced it to synonymy with *O. cellarius*. The presence of *O. cellarius* in New Zealand was recognised by Musson (1891).

The records of Taylor (1906–14 (1902–21)), Longstaff (1912), Suter (1913), Thomson (1922), and others indicate that this species was widely distributed by the early part of the twentieth century.

Biology. In its native range *O. cellarius* occurs in a variety of moist, shaded habitats such as forests, cliffs and rock walls, parks, gardens, and caves (Evans & Jones 1973, Chatfield 1975). In New Zealand it is widely established in most modified habitats, and frequently in native forests adjacent to previous or existing human settlements.

Little information is available on the life cycle of *O. cellarius* in New Zealand but for the occurrence of eggs in spring. For an English population, Rigby (1963) demonstrated an annual cycle of growth and reproduction, with a peak of adults in late winter through to early spring, and juvenile recruitment in summer. In a drought-affected year Cameron (1982) found adults to be most abundant in summer and juveniles in autumn.

The oval eggs (Fig. M123, 124), of approximately 1.5 mm greater diameter, have a whitish calcareous shell, and are deposited in clusters in the soil. Newly hatched snails have a shell diameter of 2.0–2.5 mm.

O. cellarius is omnivorous. It preys on slugs and snails and their eggs (Taylor 1902–07 (1902–21), Cotton 1954, von Proschwitz 1994; G.M. Barker, unpubl. data), earthworms (Taylor 1902–07 (1902–21)), and slaters (Cotton 1954). High numbers of *O. cellarius* occur in some native forest habitats, and observations suggest that their predatory activities contribute to decline in indigenous snail populations. The author has observed *O. cellarius* feeding on the following indigenous snails in forest: *Charopa coma* (Gray,1843), *Chaureopa roscoei* Climo, 1985, *Flammocharopa costulata* (Hutton, 1883), *Flammulina cornea* (Hutton, 1883), *Cavellia buccinella* (Reeve, 1852), *Allodiscus dimorphus* (Pfeiffer, 1853) and *Laoma mariae* (Gray, 1843).

Remarks. There has been much confusion in the New Zealand literature regarding the status of *Helix corneo-fulva* Pfeiffer, 1862. Suter (1891) considered it to be a New Zealand indigenous species, in shell form nearer to

Aegopinella nitens (Michaud, 1831) than to *O. cellarius*. Later, Suter (1904) reduced *H. corneo-fulva* to synonymy of *O. cellarius* (Müller, 1774), a decision confirmed by Climo (1984).

An introduction into the literature on *O. cellarius* is provided by Germain (1930), Pilsbry (1946 (1939–48)), Likharev & Rammel'meier (1952), Riedel (1970), Giusti (1976), Castillejo (1985), Altonaga & Puente (1991), and Giusti & Manganelli (1997).

Oxychilus (Oxychilus) draparnaudi (Beck)

Figures 62, 65, 94, 108, 135, 216, 242, C30, M106, M107; Map 27

cellarius of authors (not of Müller, 1774).
lucida Draparnaud, 1801: 96 (not of Pultney, 1799) (*Helix*).
nitida Draparnaud, 1805: 117 (not of Gmelin, 1791, nor of Müller, 1774); new name for *lucida* Draparnaud (*Helix*).
draparnauldi Beck, 1837 (1837–38): 6, an invalid original spelling for *draparnaudi* [ICZN Opinion 336, 1955b: 87]; new name for *nitida* Draparnaud (*Helix (Helicella)*).
obscurata of authors (not of Villa & Villa, 1841).
subglaba Bourguignat, 1860: 47 (*Zonites*).
corneo-fulva of authors (not of Pfeiffer, 1862).
septentrionalis Bourguignat, 1870 (1863–70): 17 (*Zonites*).
pictonica Bourguignat, 1870 (1863–70): 91 (*Zonites*).
staechadicus Bourguignat, 1877: 38 (*Zonites*).
stoechadicus Fagot, 1877: 37 (*Zonites*).
calabrica Paulucci, 1879: 44 (as variety of *Helix lucida* Draparnaud) (*Hyalinia*).
foderana Bourguignat, 1880: 107 (*Hyalinia*).
kraliki of authors (not *Zonites kraliki* Letourneux, in letter, 1878; Servain, 1880).
arcasianus of authors (not *Zonites arcasianus* Servain, 1880).
rateranus of authors (not *Zonites rateranus* Servain, 1880).
blauneri Locard, 1882: 37 (not of Shuttleworth, 1843) (*Hyalinia*).
porroi Paulucci, 1882 (1882–83): 162 (*Hyalinia*).
scotophila (not of de Stefani, 1879) var. *notha* Paulucci, 1886: 11 (*Hyalinia*).
sicula (not *Helix sicula* Benoit, 1857) var. *vulcanica* di Maria di Monterosato, 1892: 6 (*Hyalinia*).
sicula (not *Helix sicula* Benoit, 1857) var. *melitensis* di Maria di Monterosato, 1892: 6 (*Hyalinia*).
barbozana da Silva e Castro, 1894: 40 (*Hyalinia*).
gyrocurtopsis Locard, 1894: 40 (*Hyalinia*).
intermissa Locard, 1894: 41 (not *Hyalina mingrelica* Mousson var. *intermissa* Kobelt, 1879) (*Hyalinia*).
magonensis Locard, 1894: 42 (*Hyalinia*).
mauriceti Locard, 1894: 46 (*Hyalinia*).
hiulciformis Locard, 1899: 11 (*Hyalinia*).
algarvensis Locard, 1899: 12 (*Hyalinia*).
achyophila Locard, 1899: 15 (*Hyalinia*).
molleriana Locard, 1899: 16 (*Hyalinia*).
chelia Locard, 1899: 20 (*Hyalinia*).
alpina Suter, 1904: 62 (*Flammulina*).

austriaca Wagner, 1907: 114 (as a subsp. of *Helix draparnaldi*
      Beck) (*Hyalina*).
aetneus Sacchi, 1957: 656 (*Oxychilus*).
gorgonianus Giusti, 1968: 223 (*Oxychilus*).
igilicus Giusti, 1968: 230 (*Oxychilus*).

Shell (Fig. 62) of mature snails about 6 mm high by 15 mm
in diameter, strongly depressed, convex above, flattened
below, of 6–7 rather rapidly expanding whorls, with
growth lines often rather well defined and giving a slight
wrinkled appearance, especially at suture. Coloration
translucent horn brown above, paler around umbilicus
below, not very glossy. Protoconch of about 1.5 whorls,
smooth. Umbilicus about 0.13 of shell diameter. Aperture
elliptical. Columella not reflected. Peristome thin.

   Animal (Fig. 65) blue-grey, including sole, in which
central zone paler than lateral zones; mantle edge dark
grey, unspotted. Active animal with tail projecting slightly
beyond shell. Locomotion by muscular pedal waves gen-
erated at posterior of sole. Mucus colourless. Phylacites
distributed over greater part of anterodorsal body wall.
Epithelial crypts numerous and conspicuous in skin
grooves of right and dorsal aspects of anterior body.

   Reproductive system, Fig. 94. Ovotestis elongate,
composed of acini scattered along proximal hermaphrodite
duct, which is embedded in posterior lobe of digestive
gland. Hermaphrodite duct scarcely convoluted but medi-
ally distended, terminating in a diverticulate talon partially
embedded at base of linguiform albumen gland. Sperm-
oviduct narrow proximally, more ample and much folded
distally; prostatic follicles weak or absent from proximal
region but well developed distally. Free oviduct of mod-
erate length. Bursa copulatrix reservoir small, oval, on a
moderately long, slender duct. Vagina moderately long;
vaginal gland conspicuous, massed around proximal vag-
ina, concealing base of bursa copulatrix duct. Vas deferens
long and very slender, abruptly enlarged to epiphallus
after passing through muscular strands of phallus sheath.
Epiphallus somewhat twisted, slender at each extremity
but medially distended. Phallus elongate, cylindrical, en-
veloped in muscular sheath distal to pronounced medial
constriction, abruptly constricted at entry into atrium;
above insertion of epiphallus with a flagellate extension
about 0.15 length of phallus; internally lined with papillae,
these small in flagellum, mounded into pleats around entry
of epiphallus, then somewhat larger and rounded in
proximal phallus and weakly coalescing into longitudinal
folds in distal phallus. Atrium short.

   Spermatophore (Fig. 108) 3–3.5 mm long, similar in
shape to that of *O. alliarius*.

   Phallus retractor long, arising from diaphragm and with
fibres from distal part of spermoviduct, inserted at apex of
phallus flagellum.

   Jaw (Fig. 135) 1.2 mm wide, in general shape like that of
O. alliarius.

   Radula (Fig. M106, 107) with 30 transverse rows of
large teeth, each with the formula 11+2–4+C+2–4+11.
Central tooth smaller than lateral teeth, tricuspid, with
mesocone elongate and slender and ectocones weak.
Lateral teeth, usually 3 in number, tricuspid. Next tooth
transitional, lacking ectocone but frequently retaining
endocone. Marginal teeth unicuspid, aculeate, rapidly de-
creasing in size towards margin of radula.

   Digestive tract and pallial organs as for *O. alliarius*.

   Free muscle system, Fig. 216. Cephalic retractors, com-
prising buccal, left tentacular, and right tentacular stems,
arising separately from very near origin of columellar
muscle. Ocular retractors branching anteriorly to run to
ocular peduncles and inferior tentacles. Buccal retractor
not bifurcating before insertion on buccal mass. A broad,
muscular fan arising ventrally from buccal retractor stem
and penetrating lateral and ventral pedal tissues.

   Central nervous system, Fig. 242. Cerebral ganglia uni-
ted by a very short but distinct commissure. Left cerebro-
pedal connective slightly longer than the right, its length
about 1.2x width of cerebral ganglion. Pleural ganglia
close to pedal ganglia, linked to pedal and parietal ganglia
by short connectives. Visceral ganglion to right of median
plane, closely appressed to right parietal ganglion but
separated from left parietal by a short connective.

   Haploid chromosome number 24.

Type material. Described by Draparnaud (1801), with
France as type locality. Syntypes NHMW Acq. No. 1820.
xxvi.143 (6 specimens), from unknown locality.

Distribution. Native to western Europe and the Medi-
terranean. Introduced to Russia, North America, South
and North Africa, Asia, Australia, and New Zealand.

Recommended common name. Draparnaud's glass snail.

Material examined. New Zealand. ND. Waima, Jan 1990,
P.C. Mayhill. **AK.** New Lynn, Sep 1981, in greenhouses.
Ellerslie, 12 Jul 1987, B.F. Hazelwood. **WO.** Taupiri, 18 Jul
1977, in garden. Hamilton, 24 Sep 1978, in garden. Waitomo, 8
Dec 1978, under limestone rocks at roadside. **CL.** Mayor I., 8 Dec
1984, B.F. Hazelwood. **BP.** Tanners Point, Aug 1981, P.C.
Mayhill. Ohope Scenic Reserve, Aug 1977, P.C. Mayhill.
Taneatua, Sep 1980, P.C. Mayhill. Waimana, Apr 1976, under
rocks in disturbed forest. Hicks Bay, 18 Nov 1977, in remnant
coastal *Vitex lucens-Beilschmiedia tawaroa* forest. **TK.** Mokau,
Apr 1987, P.C. Mayhill, in native forest remnant. **WI.**
Nukumaru, 11 Mar 1977, F.M. Climo (MONZ M55974). **NN.**
Takaka, undated, P.C. Mayhill. Aniseed Valley, P.C. Mayhill.
Granity, May 1941, M. Holloway & A.G. Stevenson (MONZ
M84798).

History in New Zealand. *O. draparnaudi* has long been established in New Zealand but has generally been overlooked. Barker (1982) reported this species to be widely distributed, especially in the North Island. Climo (1984) showed that the *Flammulina alpina* of Suter (1904) is assignable to *O. draparnaudi*, indicating that the species has been in New Zealand since at least 1884, the year Suter's material was collected in the Nerger Range.

Biology. In Britain *O. draparnaudi* is strongly synanthropic (Kerney 1966), but little is known of its biology in New Zealand. It is most commonly encountered here in gardens, but populations are also recorded from exotic plantations, grassy wasteland, and disturbed native forest habitats. Observation of populations in gardens confirms the gregarious and strictly geophilous nature of this species, alluded to by Taylor (1906–14 (1902–21)).

Mating and egg laying have been observed during spring at several North Island localities. The eggs are oval, of 1.5 mm greater diameter, with a white calcareous shell.

According to Taylor (1906–14 (1902–21)) *O. draparnaudi* in Britain matures in the first few months of its second year, and produces 30–50 eggs during the 6-month period from spring to autumn. Similarly, Frest & Sanders Rhodes (1982) found eggs and young to be present from spring to fall in Iowa, U.S.A. In contrast, Rigby (1963) reported that English *O. draparnaudi* produces eggs during the autumn and winter months, while Rondelaud (1980) reported an annual life cycle in France, with maximum abundance of juvenile snails in spring.

O. draparnaudi is omnivorous, but with strong predatory tendencies: molluscs and their eggs can form a significant part of the diet (Rondelaud 1980, Frest & Sanders Rhodes 1982, von Proschwitz 1994). Like *O. cellarius*, this species may be implicated in the decline of indigenous snail populations in some habitats. Impact on native faunas, following introduction of *O. draparnaudi* into Iowa, has been suggested by Frest & Sanders Rhodes (1982).

Remarks. The synonymy of *Flammulina alpina* Suter, 1904 with *O. draparnaudi* (Beck, 1837) was proposed by Climo (1984).

Entry into the literature on *O. draparnaudi* is provided by Germain (1930), Pilsbry (1946 (1939–48)), Likharev & Rammel'meier (1952), Giusti (1970, 1973, 1976), Riedel (1972), Castillejo (1985), Altonaga & Puente (1991), and Giusti & Manganelli (1997).

Genus *Vitrea* Fitzinger

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Zonites of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix algira* Linnaeus, 1758, by original designation; Zonitidae.)

Helicella of authors. (Not *Helicella* of d'Audebard de Férussac, 1821, type species *Helix ericetorum* Müller, 1774 = *Helicella itala* (Linnaeus, 1758), designated by Herrmannsen (1847) [ICZN Opinion 431, 1956: 350]; Hygromiidae. Not *Helicella* of Gray, 1847, type species *Helix cellaria* Müller, 1774, by original designation – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Vitrea Fitzinger, 1833: 99, type species *Glischrus (Helix) diaphana* Studer, 1820, by monotypy [ICZN Opinion 335, 1955a: 50, 59].

Oxychilus of authors. (Not *Oxychilus* of Fitzinger, 1833, type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847); Zonitidae.)

Hyalina of authors. (Not *Hyalina* of de Charpentier, 1837, type species *Helix lucida* Draparnaud, 1801, designated by Bourguignat, 1890 – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae. Not *Hyalina* of Studer, 1820, listed in synonymy of *Vitrina* Draparnaud, 1801, Vitrinidae, by Zilch (1959–60), type designation not traced. Not *Hyalina* of Schumacher, 1817, type species *Hyalina pellucida* Schumacher, 1817, by monotypy; Gastropoda, Marginellidae. Not *Hyalina* of Rambur, 1866; Lepidoptera.)

Polita of authors. (Not *Polita* of of Held, 1837 (1837–38), type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847) – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Hyalinia of authors. (Not *Hyalinia* of Albers, 1850, type species *Helix cellaria* Müller, 1774, designated by von Martens (1860) – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Crystallus Lowe, 1855: 178 (as subgenus of *Helix* Linnaeus), type species *Helix crystallina* Müller, 1774, by monotypy.

Aplostoma of authors. (Not *Aplostoma* of Moquin-Tandon, 1855, type species *Helix cellaria* Müller, 1774, designated by Lindholm (1927) – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Discella Gray, 1857: 98, type species *Helix crystallina* Müller, 1774, by monotypy.

Euhyalina of authors. (Not *Euhyalina* of Albers, 1857, type species *Helix cellaria* Müller, 1774, by original designation – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Diaphanella Clessin, 1880b: 206, type species *Glischrus (Helix) diaphana* Studer, 1820, by original designation. (Not *Diaphanella* of Hesse, 1916, as new name for *Hydatina* Westerlund, 1886 – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae. Not *Diaphanella* of Thiele, 1912, type species *Bulla fragilis* Vélain – synonym of *Notodiaphana* Thiele, 1917; Gastropoda, Notodiaphanidae.)

Anomphala Westerlund, 1886 (1886–87): 29, type species *Glischrus (Helix) diaphana* Studer, 1820, designated by Westerlund (1902). (Not *Anomphala* Herrmannsen, 1846,

type species *Natica fluctuata* Sowerby, 1825, by original designation; Gastropoda, Naticidae.)

Crystallinus Wagner, 1907: 101, emended name for *Crystallus* Lowe.

Diagnosis. Animal able to withdraw fully into shell. Shell small, 2.5–4 mm diameter, strongly depressed, with spire slightly raised, colourless, glassy and transparent, umbilicate or imperforate, of numerous very tightly coiled whorls, not flaring towards rounded aperture; peristome thin, often with an internal callus. Animal largely vegetarian, with a tendency to predaceous feeding on snails. Buccal mass spheroidal. Jaw arched, with a broad medial projection. Radula with marginal teeth aculeate. Intestine with a single loop directed forwards. Foot narrow, with a small caudal mucous depression at posterior; sole undivided. Mantle with small shell lobes. Kidney elongate, triangular. Ureter sigmoid, closed to pneumostome. Genital orifice near right inferior tentacle. Genitalia characterised by vaginal gland enveloping proximal vagina, and a simple cylindrical phallus containing variously developed frilled or spinose stimulatory pads and a pseudopapilla not traversed by the vas deferens. Bursa copulatrix reservoir vestigial, very small, on a short, simple duct. Epiphallus absent. Right ocular retractor passing between phallus and vagina.

Haploid chromosome number 20.

Remarks. *Vitrea* is represented by over 50 species in the region from the Atlantic islands to Scandinavia, Caucasia, and Northern Africa.

Subgenus *Vitrea*

Diagnosis. Shell narrowly umbilicate or imperforate; whorls increasing gradually in diameter; aperture narrow, halfmoon-shaped.

Vitrea (Vitrea) crystallina (Müller)

Figures 66, 95, 139, 163, 189, 217, 243, C31, M29, M30, M108, M109; Map 28

crystallina Müller, 1774: 23 (*Helix*).
subterraneus Bourguignat, 1856a: 275 (*Zonites*).
humicola Mabille, 1870b: 128 (*Zonites*).
andreaei Boettger, 1880: 37 (*Hyalinia (Vitrea)*).
podolica Clessin, 1880a: 201 (*Hyalina*).
secretus Bourguignat, 1880: 25 (*Zonites*).

Shell (Fig. 66) to 4 mm in diameter by 2 mm high, strongly compressed, with spire slightly raised, of 4.5–5 closely coiled, rounded whorls, very finely and minutely striate with growth lines, slightly puckered at suture, glassy and transparent, colourless or tinged with green. Umbilicus rather narrow, about 0.12–0.15 of shell diameter, a little eccentric in last whorl. Protoconch (Fig. M29, 30) about 1.5 whorls, smooth except for very fine spiral striae, especially towards periphery. Aperture rounded, in mature specimens with a distinct internal whitish thickening or rib set back a little from sharp peristome.

Animal semi-transparent greyish white, slighter darker dorsally than at sides; mantle collar thin, transparent, finely speckled white; sole whitish; retractor muscles dark grey to black, showing through skin. Tail short, not extending beyond shell in active animal.

Reproductive system, Fig. 95. Ovotestis white, composed of acini clustered as an elongate mass embedded in digestive gland. Hermaphrodite duct moderately long, convoluted, distended medially, terminating with a diverticular talon in large albumen gland. Spermoviduct rather voluminous; prostatic follicles absent or weakly developed in proximal part but strongly developed as an elongate ribbon over the greater part. Free oviduct very short, slender. Vagina rather long, differentiated into 3 sections: proximal third very slender, like that of free oviduct; medial section broad and somewhat bulbous, its walls heavily invested with glandular tissue; distal section broad, narrowing to atrium. Bursa copulatrix reservoir a very small elliptical vesicle borne on a short, stout duct. Vas deferens long, slender, inserted in apex of phallus adjacent to attachment of phallus retractor. Epiphallus absent. Phallus elongate, cylindrical, without a sheath, internally with a small, conical to bulbous pseudopapilla near entry of vas deferens and a frilled stimulator pad in proximal section. Atrium short, slender.

Spermatophore unknown, probably not produced.

Phallus retractor arising as a branch of columellar muscle.

Jaw (Fig. 136) about 0.28 mm wide, slightly arched, with medial projection very broad and lateral extremities rounded.

Radular ribbon (Fig. M108, 109) with about 80 transverse rows of teeth, each varying around the formula 16–18+1+2+C+2+1+16–18. Central tooth on a quadrate base, tricuspid, with mesocone strong, elongate, extending beyond basal plate, and ectocones small. Lateral teeth also on quadrate basal plates, the first two tricuspid with prominent mesocone, endocone and ectocone. Third lateral tooth transitional, with a prominent endocone and mesocone, but ectocone very weak or absent. Marginal teeth elongate, unicuspid, aculeate, on slenderly rectangular to triangular basal plates, decreasing in size towards margin of radula.

Digestive tract, Fig. 163. Buccal mass slightly longer than wide. Oesophagus slender, moderately long, running directly to voluminous, cylindrical crop which occupies last third of body whorl and more than half of penultimate whorl. Stomach saccular, not constricted or externally differentiated from crop. Intestine arising from stomach between ducts of digestive gland, passing briefly along inner, columellar wall of crop before turning forwards to produce an anterior loop abutting kidney, then a short posterior loop among lobes of digestive gland, and again turning forwards to run to anus in mantle collar.

Pallial complex, Fig. 189. Pulmonary cavity occupying about 0.65 of body whorl, about 3.5x longer than wide. Kidney large, triangular, its longest axis parallel to pericardium, extending about 0.3 of length of pulmonary cavity. Ureter arising lateral to anterior apex of kidney, extending along anterior margin of kidney and then along rectum, closed to pneumostome. Vascularisation of mantle roof poorly developed. A glandular mass occupying anterior mantle roof adjacent to mantle collar.

Free muscle system, Fig. 217. Cephalic retractors, comprising buccal, left tentacular, and right tentacular stems, arising separately from very near origin of columellar muscle. Ocular retractors branching anteriorly to run to ocular peduncles and inferior tentacles. Buccal retractor bifurcating shortly before its insertion on buccal mass. A broad, muscular fan arising ventrally from buccal retractor to penetrate lateral and ventral pedal tissues.

Central nervous system, Fig. 243. Cerebral ganglia united by a very short but distinct commissure. Left cerebropedal connective markedly longer than the right, its length about 2x width of cerebral ganglion. Pleural ganglia united to pedal and parietal ganglia by short connectives. Visceral ganglion, closely appressed to right parietal ganglion but separated from left parietal by a short connective, lying to right of median plane.

Haploid chromosomes number 20.

Type material. The whereabouts of the type specimens, from near Copenhagen, Denmark, is unknown.

Distribution. Throughout the British Isles, western and central Europe, Scandinavia, and northern Africa. Introduced to South Africa, Australia, and New Zealand.

Recommended common name. Crystal snail.

Material examined. New Zealand. ND. Waipu Caves, 7 Aug 1978, B.F. Hazelwood (MONZ M68407). AK. Hoteo, 20 Apr 1987, B.F. Hazelwood & H. Taylor. Auckland Domain, Aug 1986, J.F. Goulstone. Orakei, 25 Oct 1987, J.F. Goulstone, in scrubland on coastal cliff. Ellerslie, 4 Apr 1987 and 12 Jul 1987,

B.F. Hazelwood. CL. Opoutere, 29 May 1996, G.M. Barker & M.P. Barker, in grass at road side. WO. Limestone Downs, Feb 1992, under limestone rocks in pasture. Hamilton, 5 May 1978, in garden. Ohaupo, 2 Aug 1987, in pasture. HB. Pukeora Hill, Waipukurau, 8 Mar 1977, B.F. Hazelwood (MONZ M55778). NN. Takaka, Gorge Creek, Jan 1975, P. Jamieson (NMZ M37683). Takaka Hill, Feb 1981, P.C. Mayhill. Motueka, 6 Oct 1994, under driftwood on coastal bank. BR. Woodpecker Bay, 30 Jan 1983, D.J. Roscoe (MONZ M89704). DN. Purakauri, 1985, R. Wallace, midden (NMZ M85801).

Extralimital. England. Colt Park Wood, Malham, Yorkshire, 1977, coll. & det. R.A.D. Cameron.

History in New Zealand. First recorded from New Zealand by Crosse (1893), without a locality. Known only from Auckland in the early part of the twentieth century (Suter 1913, Thomson 1922). Now widely distributed in New Zealand but poorly represented in collections.

Biology. Knowledge of this species, summarised by Taylor (1906–14 (1902–21)) and Kuiper (1964), is very sparse, owing principally to its litter-dwelling and subterranean habit restricting observations of the living animal, but also to its confusion with *V. contracta* (Westerlund, 1871). In its native European range *V. crystallina* is characteristic of moist sites such as wet grassland, marshes, stream banks, and woods (e.g., Kerney & Cameron 1979), and caves (Evans & Jones 1973). It is tolerant of oligotrophic conditions such as occur in peat bogs. The snails form a thin, transparent epiphragm to adhere to sand grains and other small particles, and thus close over the shell aperture to conserve moisture.

V. crystallina feeds upon decaying vegetable matter and preys on other small snails.

Remarks. In the older literature *V. crystallina* had often not been distinguished from *V. contracta*. Many early authors regarded *V. contracta* as a variety of *V. crystallina* or as being synonymous with it. Summaries of characters distinguishing *V. crystallina* and *V. contracta* are provided by Kuiper (1964), Kerney & Cameron (1979), and Altonaga (1989a).

Entry into the literature on *V. crystallina* is provided by Germain (1930), Likharev & Rammel'meier (1952), Kuiper (1964), Pintér (1968, 1972), and Altonaga (1989a).

Subfamily GASTRODONTINAE

Diagnosis. Zonitidae in which the shell is globulose to strongly depressed, umbilicate, the aperture frequently with barriers or an internal callus. Sole uniform; progression not by muscular waves but arhythmic. Genital orifice

situated a considerable distance from right ocular peduncle. Phallus with a dart sac containing a dart (sometimes absent in minute forms) and an epiphallus. From a sheath around base of phallus a duct runs to free oviduct, either directly (*Gastrodonta*, *Janulus*) or indirectly by way of anterior part of bursa copulatrix duct (*Zonitoides*, *Ventridens*). Phallus, oviduct, and bursa copulatrix duct arising from rather long atrium in close proximity; vagina very short or absent. Right ocular retractor passing to left of genitalia. Radula with lateral teeth lacking endocones, bicuspid or unicuspid; outer marginal teeth unicuspid, aculeate.

Remarks. A discussion on the nomenclatural history and generic characteristics of Tryon's subfamily Gastrodontinae is provided by Pilsbry (1946 (1939–48)).

The subfamily is primarily North American, and comprises the following genera (Zilch 1959–60): *Gastrodonta* Albers, 1850; *Janulus* Lowe, 1852; *Zonitoides* Lehmann, 1862; *Striatura* Morse, 1864; *Ventridens* Binney & Bland, 1869; *Poecilozonites* Boettger, 1884. Represented in New Zealand by a single naturalised species.

Genus *Zonitoides* Lehmann

Helix of authors. (Not *Helix* of Linnaeus, 1758, type species *Helix pomatia* Linnaeus, 1758, designated by de Montfort (1810); Helicidae.)

Zonites of authors. (Not *Zonites* of de Montfort, 1810, type species *Helix algira* Linnaeus, 1758, by original designation; Zonitidae.)

Omphalina of authors. (Not *Omphalina* of Rafinesque Schmaltz, 1831, type species *Omphalina cuprea* Rafinesque Schmaltz, 1831, by monotypy; Zonitidae.)

Oxychilus of authors. (Not *Oxychilus* of Fitzinger, 1833, type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847); Zonitidae.)

Hyalina of authors. (Not *Hyalina* of de Charpentier, 1837 (as subgenus of *Helix* Linnaeus), type species *Helix lucida* Draparnaud, 1801, designated by Bourguignat (1890) – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae. Not *Hyalina* of Studer, 1820, listed in synonymy of *Vitrina* Draparnaud, 1801, Vitrinidae, by Zilch (1959–60), type designation not traced. Not *Hyalina* of Schumacher, 1817, type species *Hyalina pellucida* Schumacher, 1817, by monotypy; Gastropoda, Marginellidae. Not *Hyalina* of Rambur, 1866; Lepidoptera.)

Polita of authors. (Not *Polita* of Held, 1837 (1837–38), type species *Helix cellaria* Müller, 1774, designated by Herrmannsen (1847) – synonym of *Oxychilus* Fitzinger, 1833; Zonitidae.)

Zonitoides Lehmann, 1862: 111, type species *Helix nitida* Müller, 1774, by monotypy [ICZN Opinion 335, 1955a: 50, 59].

Zonitellus Baker, 1928: 37, type species *Helix arboreus* Say, 1816, by original designation.

Alienitor Iredale, 1937: 6, type species *Helix lyndhurstensis* Cox, 1868 = *Helix arboreus* Say, 1816, by original designation.

Diagnosis. Herbivorous species. Animal able to withdraw fully into shell. Shell small, diameter 4–8 mm, thin, depressed, umbilicate, lightly or distinctly striate above, rarely ribbed, composed of 3.5–4.5 convex, regularly increasing whorls; aperture rounded, lunate; lip thin, with no internal callus or barrier. Foot long and narrow, with distinct pedal grooves and a narrow slit-like caudal pit. Buccal mass spheroidal. Jaw oxygnathic, with a central projection. Radula with marginal teeth elongate, bicuspid or unicuspid. Intestine with a single loop directed forwards. Genital orifice just above pedal groove, slightly behind anterior edge of visceral stalk. Genitalia characterised by a rather long atrium into which open free oviduct, bursa copulatrix, and phallus. Male genitalia with a short apical epiphallus and usually a large lateral dart sac bearing 1 or 2 coronal glands. Bursa copulatrix duct bifurcate, one branch running to atrium, the other to base of phallus. Left cerebropedal connective longer that the right, its length 1.5–2× width of cerebral ganglion. Pleural ganglia close to pedal ganglia, on short but distinct pleural–pedal connectives. Visceral chain compact, but ganglia never fused. Haploid chromosome number 30.

Remarks. Practically Holarctic in distribution. Several species have been widely distributed through the activities of man.

Two subgenera were recognised by Pilsbry (1946 (1939–48)), *Zonitoides* Lehmann s.s. and *Pseudohyalus* Baker, 1929.

Subgenus *Zonitoides*

Diagnosis. Shell glossy, with only weak sculpture.

Zonitoides (Zonitoides) arboreus (Say)

Figures 67, 96, 137, 164, 190, 218, 244, C32, M31, M110–112, M125, M126; Map 29

arboreus Say, 1816: pl. 4, fig. 4 (*Helix*).
ottonis, Pfeiffer, 1840: 251 (*Helix*).
breweri Newcomb, 1864: 118 (*Helix*).
whitneyi Newcomb, 1864: 118 (*Helix*).
lyndhurstensis Cox, 1868: 11 (*Helix*).
viridula Cockerell, 1888: 257 (as var. of *arboreus* Say) (*Hyalina*).
roseni Lindholm, 1911: 98 (*Hyalina (Polita)*).
lyndhurstoides McLaughlan, 1954: 40 (*Alienitor*).

Shell (Fig. 67) up to 3 mm high by 6 mm in diameter, depressed, of about 4.5 moderately convex and regularly increasing whorls, translucent olive buff, glossy in appearance but weakly sculptured with growth wrinkles and extremely faint, minute spiral striae, the base smoother. Protoconch (Fig. M31) of 1.5 whorls, smooth but for microscopic growth lines and spiral striae at periphery. Umbilicus about 0.2 of shell diameter. Aperture deeply lunate, wider than high. Columella scarcely reflected. Peristome thin.

Animal bluish-grey to blackish above and on ocular peduncles and inferior tentacles, paler and often speckled brown or white towards foot edges; mantle collar slate grey flecked with white; sole white or grey. Active animal with tail long, extending beyond posterior limit of shell. Locomotion arhythmic.

Reproductive system, Fig. 96. Ovotestis consisting of 3 groups of clavate acini embedded in digestive gland. Hermaphrodite duct weakly convoluted, terminating in albumen gland with a bulbous diverticular talon. Albumen gland large. Spermoviduct sacculately swollen, particularly at distal end; prostatic gland long, but alveoli absent at proximal end. Free oviduct rather long. Bursa copulatrix reservoir spherical, on a long, slender duct which bifurates anteriorly to atrium and base of phallus. Vas deferens short, slender, passing directly to slender apex of epiphallus. Epiphallus broadening to attachment with phallus; entry to phallus with a large, conical vergic papilla partially invested by a curved, calcareous plate. Phallus differentiated into a vergic compartment, a dart sac, and a short preputial section; vergic sac short, cylindrical, with weak longitudinal pilasters; dart sac at least twice as long as vergic sac, its apical part containing the dart-papilla usually recurved and marked off by a slight constriction, bearing laterally a bifurcate coronary gland; dart approx. 1.78 mm long, slender, weakly curved. Phallus vergic sac and preputium surrounded by a muscular sheath. Atrium short, stout.

Spermatophore unknown.

Phallus retractor long and slender, arising from diaphragm, inserted to side of phallus vergic sac apex. Dart retractor arising from fork of bursa copulatrix duct, inserted at apex of dart sac.

Jaw (Fig. 137) about 0.4 mm wide, with a strong anteromedial projection.

Radular ribbon (Fig. M110–112) with about 76 transverse rows of teeth, each with the formula 19+6+1+6+19. Central tooth noticeably larger than first laterals, tricuspid, with an elongate mesocone and small ectocones, on quadrate basal plate. Lateral teeth bicuspid, with an elongate mesocone and small ectocone, on quadrate basal plates. Marginal teeth elongate, sword-like, unicuspid, on elongate basal plates.

Digestive tract, Fig. 164. Buccal mass spheroidal. Oesophagus long and slender; crop absent. Stomach extending about 0.4 of a whorl, cylindrical, broadening to gastric pouch, with 2 ducts to digestive gland. Intestine with a short, anteriorly directed loop abutting kidney before producing a short posterior loop embedded in digestive gland, then finally running forwards to anus in mantle collar.

Pallial complex, Fig. 190. Pulmonary cavity nearly 3x longer than wide, extending in live animal to about 0.7 of body whorl, with weak but distinct venation. Kidney triangular, its greater axis parallel to lung axis. Ureter sigmoid, considerably distended, closed to pneumostome.

Free muscle system, Fig. 218. Columellar muscle subtending near its origin separate branches to buccal mass and right cephalic region, the latter promptly dividing into tentacular and somewhat heavier lateral retractors; left tentacular retractor branching off more anteriad from stem which forms combined left lateral retractor and tail retractor. Right ocular retractor crossing over phallus to reach ocular peduncle.

Central nervous system, Fig. 244. Cerebral ganglia united by a short but distinct commissure. Cerebropedal connectives long, exceeding 1.5x width of cerebral ganglion; right connective shorter than the left. Pleural ganglia closer to pedal ganglia than to cerebral ganglia. Visceral chain compact, but ganglia neither closely appressed nor fused together. Visceral ganglion lying to right of median plane.

Haploid chromosome number unknown.

Type material. Described from North America without precise type locality; Baker (1933) thought that Say's material originated from Philadelphia.

Distribution. Z. *arboreus* appears to be native over the entire Nearctic region, extending to the tropics of Central America. Introduced into Hawaii, Israel, Kenya, South Africa, Madagascar, Mauritius, Hong Kong, South America, Europe, Madeira, Scandinavia, Russia, Australia, and New Zealand.

Recommended common name. Orchid snail.

Material examined. New Zealand. ND. Whangarei, 12 Sep 1983, G. Peake, in orchids. AK. Auckland, Nov 1959, L. Laird, infesting *Cattleya* orchids. Mairangi Bay, 29 Aug 1994, K.E. Fletcher, on *Portulaca oleracea*. New Lynn, 20 Jan 1985, J. Cole (MONZ). Ellerslie, 15 Aug 1977, in nursery; May 1978, B.F. Hazelwood. Mt Wellington, B.F. Hazelwood. Mangere, 19 Oct 1982, S. Reynolds & R. Kleinpaste, in nursery. CL. Mayor I., Feb 1991, P.C. Mayhill. WO. Ohaupo, 8 Jul 1988 and 3 Feb 1991, in

greenhouse orchids. Cambridge, 16 Mar 1984, S. Wathen, in orchids. Matamata, 21 Mar 1994, in greenhouse orchids. Karapiro, May 1989, infesting potted ferns in heated greenhouses. **BP**. Omokoroa, 4 Oct 1991, P.C. Mayhill. **HB**. Napier, 5 Mar 1963, R. Cumber (MONZ M17982). **TK**. New Plymouth, 1 Sep 1993, G.J. Dunn. **WA**. Eketahuna, 1970, D.J. Roscoe, in orchid nursery (MONZ M98187). **WN**. Wellington, Dec 1952, B.T. Giles (MONZ). **MC**. Christchurch, 26 Oct 1991, F.S. Fox.

Extralimital. Australia. Emerald, Queensland, Aug 1992, under logs in opencast mine area. Camben, New South Wales, 16 Oct 1993, in gardens. **England**. Kew, Royal Botanic Gardens, London, 9 Sep 1990, in greenhouses.

History in New Zealand. Recorded in New Zealand under the name *Zonitoides nitida* (Müller, 1774) by Cotton (1954). The earliest New Zealand collection date for material examined in this study was 1952.

Biology. In its native range *Z. arboreus* occurs from sea level to altitudes of about 3800 m (Bequaert & Miller 1973). Primarily a woodland or forest snail, *Z. arboreus* has become widely established in cultivated habitats in North America (Goodrich & van der Schalie 1944, Robertson & Blakeslee 1948, Hubricht 1985) and, as a consequence, has been distributed to many parts of the world with plant material. In particular it is associated with greenhouse floricultural crops (Meeuse & Hubert 1949, Karlin 1956, Karlin & Naegele 1960, Kerney & Cameron 1979), where it can be a significant pest (Karlin & Naegele 1960, Davidson 1962, Chadwick 1970, Moens 1977, Moran & Katzir 1979, Verdcourt 1979, Mienis 1980, Barker 1986).

In New Zealand this species is largely confined to greenhouses, where it is frequently found damaging tender plants such as orchids and ferns (Barker 1986, Martin & Workman 1988). In northern areas such as Whangarei, Auckland, and Hamilton *Z. arboreus* has also established outdoors in gardens.

The biology of *Z. arboreus* has been studied in New Zealand orchid houses and in the laboratory by Dr J. Dymock, who kindly provided the following information. Snails reach sexual maturity at a shell width of 3.6 mm. Fertile eggs can be produced from self-fertilisation. The eggs, about 1 mm in diameter and white, owing to a calcareous shell (Fig. M125, 126), are laid in clutches of 4–6 in damp litter and bark potting medium. The duration of the egg stage ranges from 5 to 9 days at 25^{0}C. The period from eclosion to egg production for snails reared in a bark medium on lettuce diet ranges from 25 weeks at 15^{0}C, through 8 weeks at 20^{0}C, to 5 weeks at 25^{0}C. The lower threshold for development was estimated to be 12.5^{0}C.

There were no seasonal trends in age-class distribution (measured by shell width) in snail populations in greenhouse orchids. All sizes of snail were found to be present at any one time, and there was no apparent synchronisation in size distribution from one greenhouse to the next.

Bartsch & Quick (1926) recorded cross-fertilisation in *Z. arboreus*, where by "... one animal acts as male only and the other as female only. There is, therefore, not a reciprocal fertilization ....".

Remarks. Entry into the literature on *Z. arboreus* is provided by Pilsbry (1946 (1939–48)), Likharev & Rammel'meier (1952), Waldén (1953), and Bequaert & Miller (1973).

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KEY TO EXOTIC TERRESTRIAL SLUGS AND SNAILS NATURALISED IN NEW ZEALAND

This key provides for species determination of naturalised taxa, and is not systematic. For snails, shells of mature specimens are required for proper function of the key. Indigenous taxa were not taken into account in the development of this key, and hence are unlikely to key out.

1 Animal with an external shell ... 2
— Animal without an external shell ... 17

2(1) Shell reduced, incapable of housing the retracted animal, auriform, situated at posterior of body. Animal slug-like ... (p. 98; Fig. 56, 57, C25) .. ***Testacella haliotidea***
— Shell capable of housing the retracted animal ... 3

3(2) Shell conical, cylindrical, elongate-oval or lanceolate, its height clearly greater than its diameter ... 4
— Shell flattened or globose, its height equal to or less than its diameter ... 8

4(3) Shell cylindrical-oval, with apertural teeth ... 5
— Shell elongate-oval or lanceolate, lacking apertural teeth ... 6

5(4) Shell less than 6 mm in height; last whorl less than half shell height; aperture usually with a single lamella; yellowish brown to reddish brown; translucent and glossy, with delicate transverse striation ... (p. 95; Fig. 55, C24) .. ***Lauria cylindracea***
— Shell less than 3 mm in height; last whorl more than half shell height; aperture with 3 to (usually) 5 teeth; yellowish brown to chestnut; glossy to mat, with fine growth lines... (p. 105; Fig. 59, C27) .. ***Vertigo ovata***

6(4) Shell conical, 8–12 mm in height, slightly glossy, white to pale brown, generally profusely streaked, flecked, or banded with buff; umbilicus minute, partially closed by reflection of columella ... (p.75; Fig. 40, C13) .. ***Prietocella barbara***
— Shell lanceolate or elongate-oval, less than 8 mm in height, glossy, colourless or brown, without pattern; imperforate ... 7

7(6) Shell elongate-oval, less than 8 mm in height; apex bluntly pointed; aperture subvertical, oval, with smooth callous rib inside; yellowish corneous ... (p. 52; Fig. 34, C8) .. ***Cochlicopa lubrica***
— Shell lanceolate, less than 5 mm in height; apex rounded, blunt; aperture narrow, vertically directed; colourless... (p. 59; Fig. 36, C9) .. ***Cecilioides acicula***

8(3) Shell globose – height and diameter about equal ... 9
— Shell subglobose to strongly flattened – height clearly less than diameter, less than 15 mm ... 10

9(8) Shell 3–6 mm in height; umbilicus partially closed by reflection of columella; corneous to horn-coloured ... (p. 56; Fig. 35) .. ***Coneuplecta calculosa***
— Shell 20–40 mm in height; dull yellow with solid or broken brown bands; imperforate ... (p. 62; Fig. 37, C10, C11) .. ***Cantareus aspersus***

10(8) Shell subglobose, up to 14 mm in diameter; thick, with coarse radial ribbing; periphery of whorls slightly angled; opaque buff to pale brown with darker continuous or broken bands ... (p. 73; Fig. 39, C12) .. ***Candidula intersecta***
— Shell discoidal, rather thin, without coarse radial ribbing ... 11

11(10) Shell less than 4 mm in diameter ... 12
— Shell more than 4 mm in diameter ... 14

12(11) Shell with an umbilicus less than 0.2x its diameter; transparent, colourless, or tinged green; glossy, with faint growth lines; aperture rounded, with an internal whitish callous rib ... (p. 117; Fig. 66, C31) .. ***Vitrea crystallina***
— Shell with umbilicus equal to or greater than 0.2x its diameter; aperture without an internal white callous rib ... 13

13(12) Shell less than 2.5 mm in diameter; aperture lunate; peristome not thickened or reflected; transparent, pale straw to white; glossy, with faint growth lines ... (p. 69; Fig. 38) .. ***Helicodiscus singleyanus***
— Shell less than 2.5 mm in diameter; aperture circular; peristome abruptly thickened but weakly reflected to form a white lip; translucent white to straw coloured; glossy, with faint growth lines ... (p. 100; Fig. 58, C26) .. ***Vallonia excentrica***

14(11) Shell less than 10 mm in diameter, with 4–5 moderately to strongly depressed whorls ... 15
— Shell 10–15 mm in diameter, with 5–7 strongly depressed whorls ... 16

15(14) Shell whorls strongly depressed, convex above, flattened below; translucent, pale yellowish brown above, paler below; glossy, with faint, rather regular growth lines. Animal with tripartite sole and phylacites densely clustered on body wall immediately anterior to mantle collar; (usually) smelling of garlic when disturbed; genitalia lacking dart apparatus ... (p. 109; Fig. 60, 63, C28) .. ***Oxychilus alliarius***

—Shell whorls slightly compressed, with a hint of keeling at periphery; translucent, olive buff; glossy, weakly scruptured with growth wrinkles and microscopic spiral striations. Animal with sole not tripartite and lacking phylacites; not smelling of garlic when disturbed; genitalia with dart apparatus
... (p. 119; Fig. 67, C32) .. *Zonitoides arboreus*

16(14) Shell with whorls regularly increasing in breadth; translucent yellow or brown, paler below; glossy, with faint irregular growth lines. Animal with phylacites over most of anterodorsal body wall but lacking crypts; phallus divided into proximal and dorsal sections by a poorly defined medial constriction
... (p. 111; Fig. 61, 64, C29) .. *Oxychilus cellarius*
—Shell with last whorl distinctly broader than penultimate whorl; last quarter-whorl often slightly downturned and compressed; translucent brownish-yellow, paler below; not usually very glossy, with well defined growth lines giving wrinkled appearance. Animal with anterodorsal body wall largely covered with phylacites and with numerous crypts in skin grooves on the right; phallus divided into proximal and dorsal sections by a well defined medial constriction
... (p. 114; Fig. 62, 65, C30) .. *Oxychilus draparnaudi*

17(1) Animal with oval mantle shield situated anterodorsally on body, containing internally granular shell fragments; pneumostome in right anterior margin of mantle shield; caudal mucus gland present   ... 18
—Animal with elongate-oval mantle shield anterodorsally on body, containing internally an oval shell plate; pneumostome in right posterior margin of mantle shield; caudal mucus gland absent   ... 20

18(17) Animal up to 25 mm in extended length; body and mantle shield yellow to pale grey, (usually) with a grey band on either side; sole yellowish grey, with yellow mucus. Genitalia with free oviduct short, not eversible
... (p. 48; Fig. 33, C6, C7) .. *Arion intermedius*
—Animal 25–50 mm in extended length; body and mantle shield yellowish grey to black, with a band on either side; sole pale yellow to orange, with sticky yellow-orange mucus. Genitalia with free oviduct long   ... 19

19(18) Dorsum of body dark brown to (more usually) yellowish grey, with dark lateral bands; band on right side of mantle shield enclosing pneumostome, often with a small break immediately dorsal to pneumostome. Genitalia with free oviduct bipartite or (usually) tripartite, its broad distal section (when present) eversible as a slender process during copulation; entry

of epiphallus to atrium with a conical verge; spermatophore slender, with a smooth to weakly serrate longitudinal ridge   ... (p. 43; Fig. 31, C4)
.. *Arion distinctus*
—Dorsum of body grey to (more usually) dark brown or black, with a dark lateral band; band on right side of mantle shield arching over pneumostome. Genitalia with free oviduct tripartite, its broadly conical distal section eversible as a slender process during copulation; entry of epiphallus to atrium with an elongate oval verge; spermatophore stout, with a strongly serrate longitudinal ridge   ... (p. 45; Fig. 32, C5)
.. *Arion hortensis*

20(17) Mantle shield bearing a horseshoe-shaped groove; dorsal keel of body extending to posterior margin of mantle shield; genitalia with epiphallus well developed, producing elaborately spinose spermatophores
... 21
—Mantle shield lacking a horseshoe-shaped groove; dorsal keel of body not extending to mantle shield posterior margin; genitilia lacking an epiphallus... 23

21(20) Body with grooves between tubercles mostly unpigmented; pneumostome without a pale border; mucus colourless; genitalia with atrium equipped with accessory glands and housing a long stimulator
... (p. 87; Fig. 49, 52, C20, C21) .. *Milax gagates*
—Body with grooves between tubercles pigmented; pneumostome with a pale border; mucus yellow or orange; genitalia equipped with accessory glands on distal portion of vagina, but lacking an atrial stimulator   ... 22

22(21) Body dull yellow-grey or brown, densely sprinkled and lineolated with black; dorsal keel yellowish or grey; pneumostome with an inconspicuous pale grey border; genitalia with paired, lobate accessory vaginal glands   ... (p. 90; Fig. 50, 53, C22)
.. *Tandonia budapestensis*
—Body pale to dark brown, with darker speckling; dorsal keel pale yellow or orange, without speckling of dark pigment; pneumostome with a pale border; genitalia with numerous tubular accessory vaginal glands and several folds in atrium   ... (p. 92; Fig. 51, 54, C23)
.. *Tandonia sowerbyi*

23(20) Body speckled, flecked, mottled, or nearly unpatterned, but never with bands; tail obliquely truncated; posterior of mantle shield rounded; right ocular retractor to left of terminal genitalia; intestine with 1 forward-directed loop   ... 24

—Body banded or spotted; tail pointed but not truncated; posterior margin of mantle shield obtusely angled; right ocular retractor passing over phallus; intestine with 2 forward-directed loops ... 26

24(23) Animal up to 50 mm long, stout, generally whitish or creamy with darker markings; mucus normally colourless, but milky when animal disturbed; rectum with a caecum ... (p. 38; Fig. 27, 30, C3)
.. Deroceras reticulatum
—Animal up to 30 mm long, slim, generally dark grey or brown, finely speckled or flecked with black; mucus colourless; rectum without a caecum ... 25

25(24) Pneumostome without a pale border. Phallus elongate, its proximal apical part with several small papillae, its distal part internally with a small hemispherical to conical sarcobelum; phallus often reduced or absent... (p. 32; Fig. 25, 28, C1) *.. Deroceras laeve*
—Pneumostome with a conspicuous pale border. Proximal phallus with 4–6 slender flagella located in a shallow recess between phallus lobe and digitiform caecum; distal phallus bulbous, internally with a large conical sarcobelum ... (p. 35; Fig. 26, 29, C2)
.. Deroceras panormitanum

26(23) Mantle shield with 2 lateral bands and a more-or-less conspicuous central band ... 27
—Mantle shield spotted or mottled, but never with longitudinal bands ... 28

27(26) Animal 40–60 mm long. Body pale greyish yellow to greyish brown, overprinted with brown or black bands; mantle shield with lateral bands and a diffuse central band; back with 1 or 2 pairs of more-or-less visible lateral bands. Phallus cylindrical, elongate, lacking an appendix ... (p. 78; Fig. 41, 45, C14, C15)
.. Lehmannia nyctelia
—Animal 60–75 mm long. Body pale greenish yellow, brown, or reddish, overprinted with brown bands and mottling; mantle shield with a median band, 2 conspicuous lateral bands, and a spotted or mottled lateral and anterior margin; back usually with a band on either side and, below this, either spotted or with diffuse lower bands. Phallus cylindical, short, with a lateral appendix ... (p. 79; Fig. 42, 46, C16)
.. Lehmannia valentiana

28(26) Animal 100–120 mm long; back and mantle shield greyish or greenish with paler spots. Rectum with a long caecum. Duct of bursa copulatrix opening to free oviduct ... (p. 81; Fig. 43, 47, C17, C18)
.. Limacus flavus
—Animal 100–200 mm long; back pale brown or grey with 4–6 more-or-less interrupted dark bands; mantle shield spotted. Rectal caecum absent. Duct of bursa copulatrix opening to base of phallus ... (p. 84; Fig. 44, 48, C19) *.. Limax maximus*

ILLUSTRATIONS
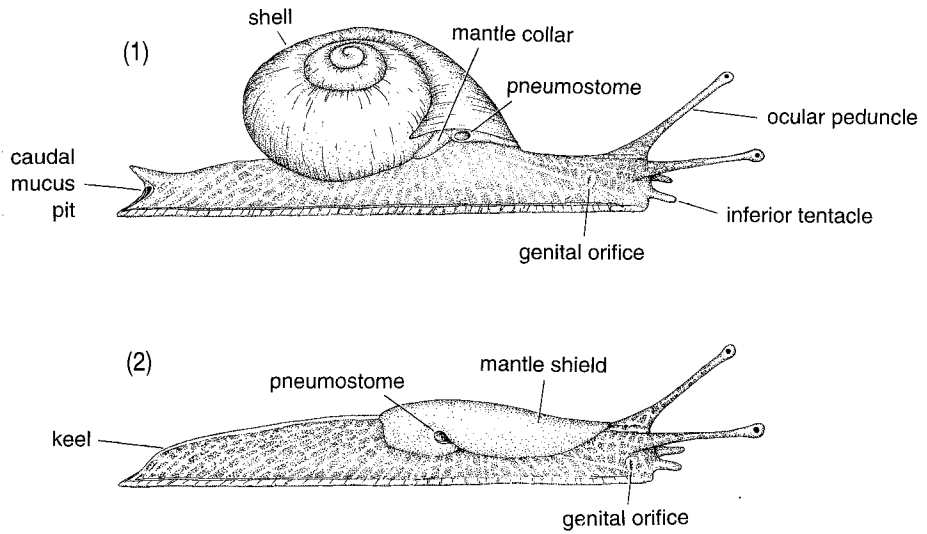
Fig. 1, 2 Generalised lateral habitus of Stylommatophoran snail and slug.
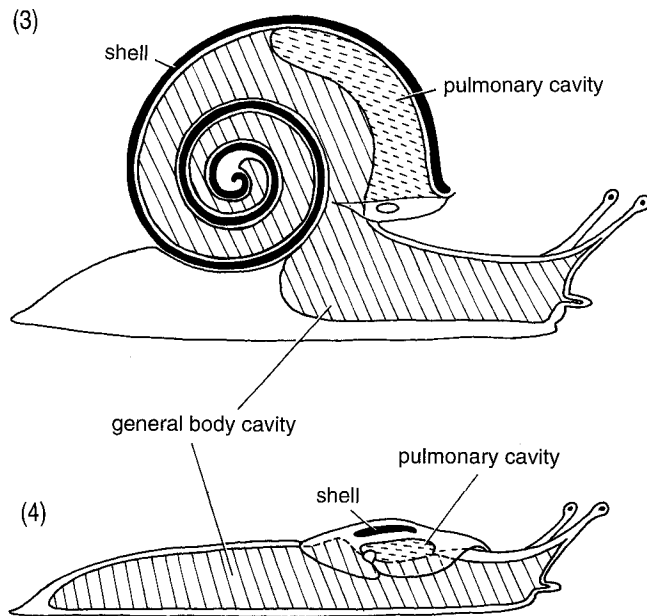
Fig. 3, 4 schematic longitudinal sections of Stylommatophoran snail and slug, showing extent of general body cavity and pulmonary cavity.
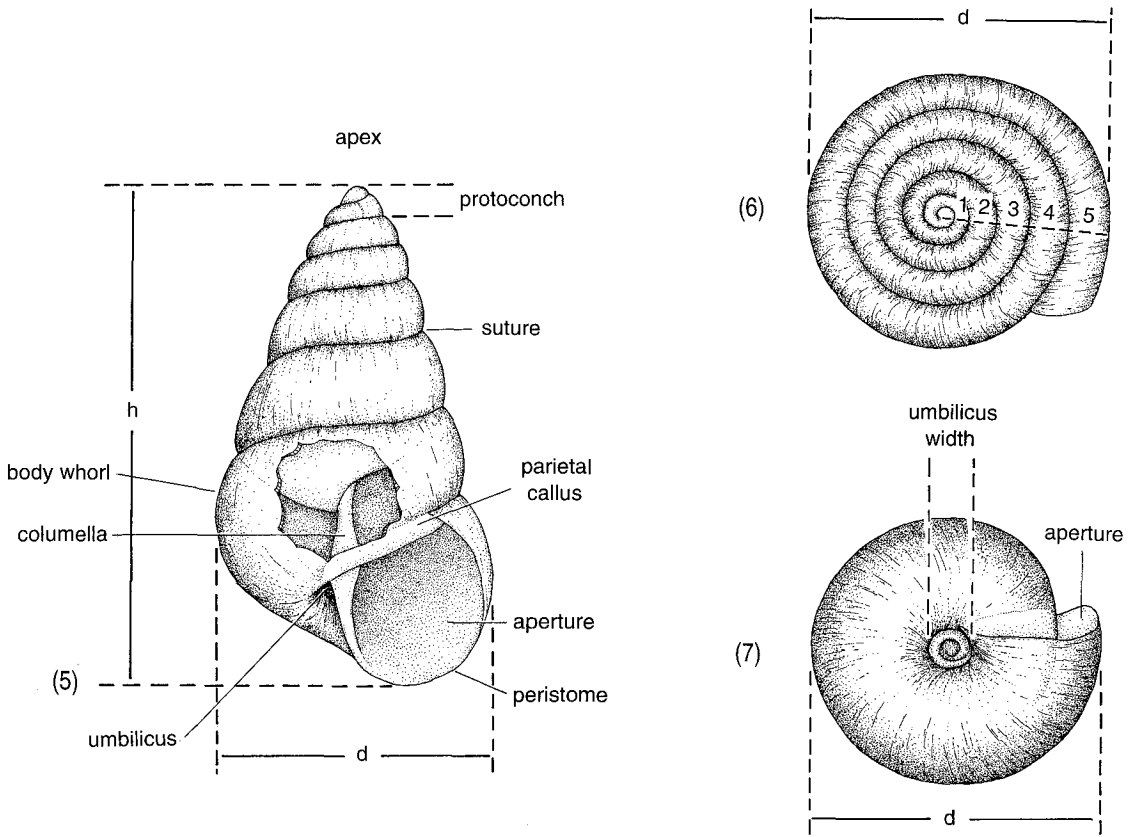
Fig. 5–7 Generalised stylommatophoran shell, in lateral, dorsal, and ventral aspect, illustrating features useful in taxonomy. Key: d, diameter; h, height; 1–5, shell whorls.
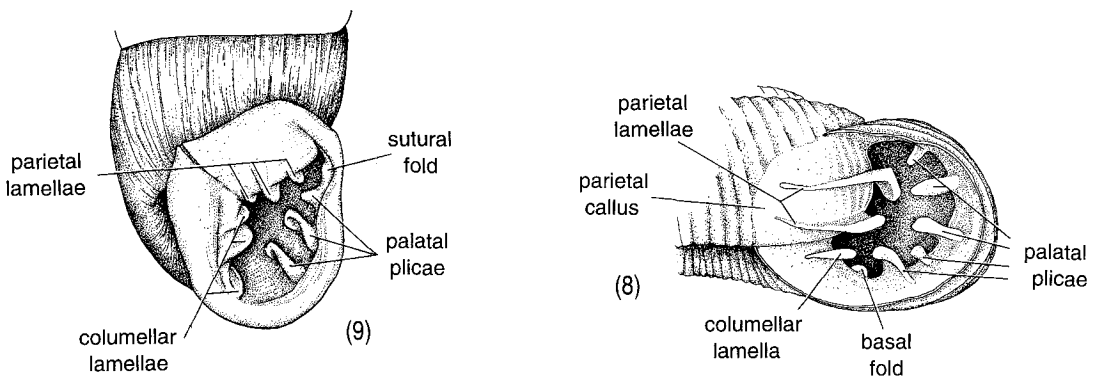
Fig. 8, 9 Shell aperture from two stylommatophoran species, illustrating terminology applied to apertural barriers.
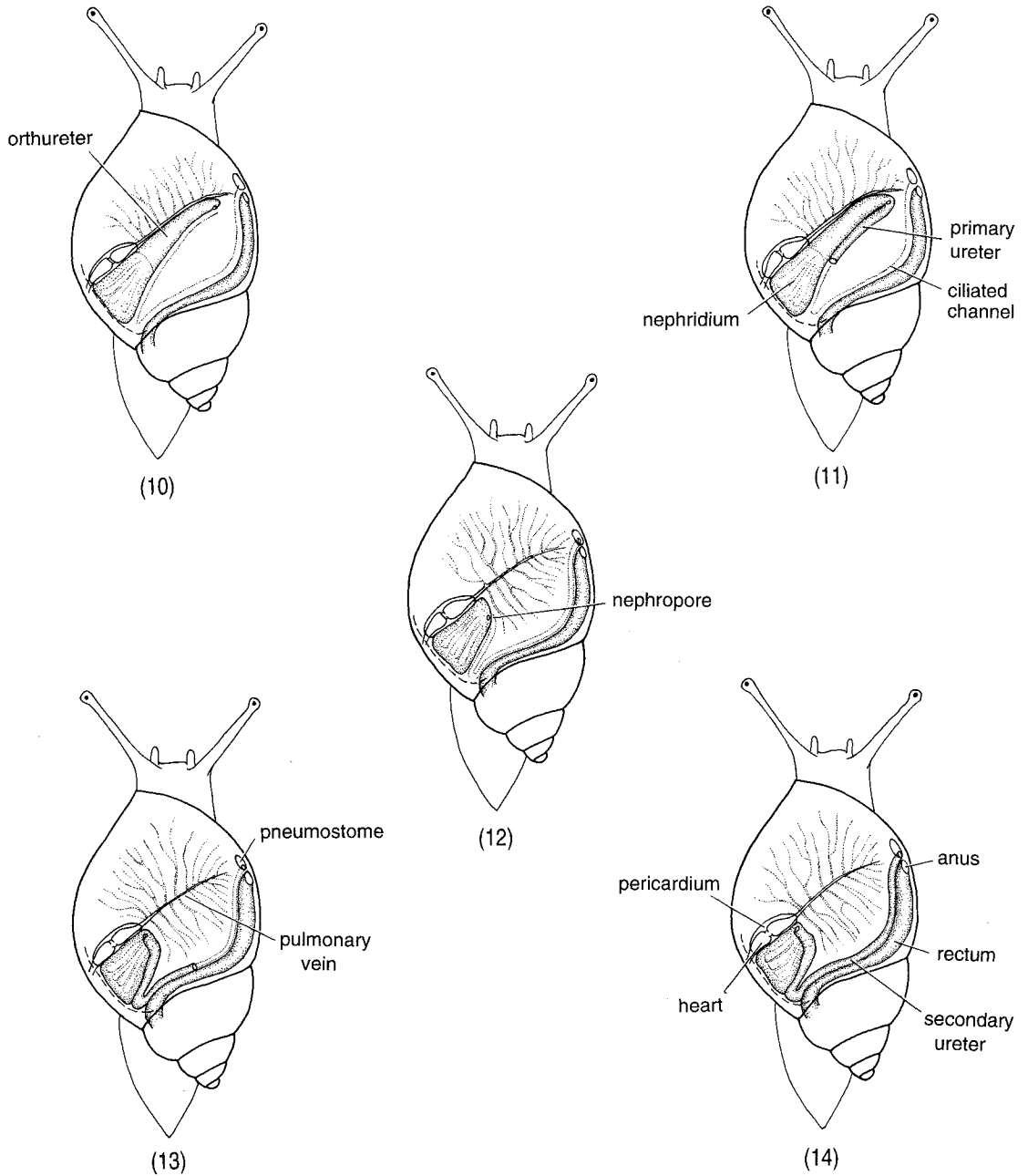
Fig. 10–14 Variation in arrangement of pulmonary and excretory organs in the stylommatophoran pulmonary cavity (semi-schematic), representative of taxa referred to Orthurethra (10, 11), Mesurethra (12), and Sigmurethra (13, 14).
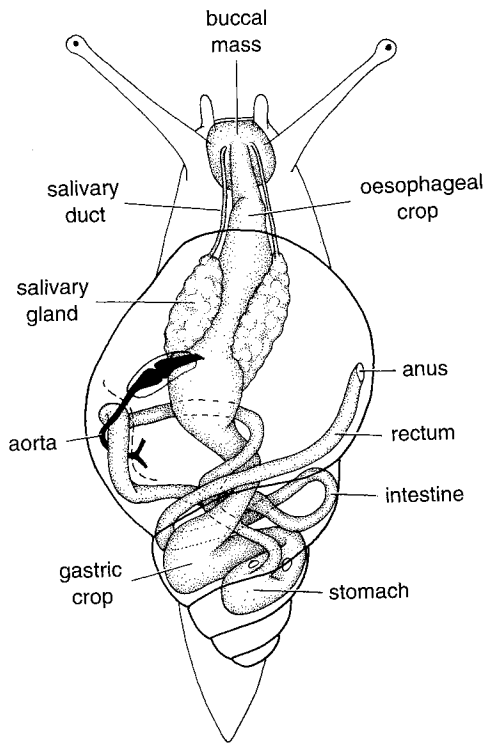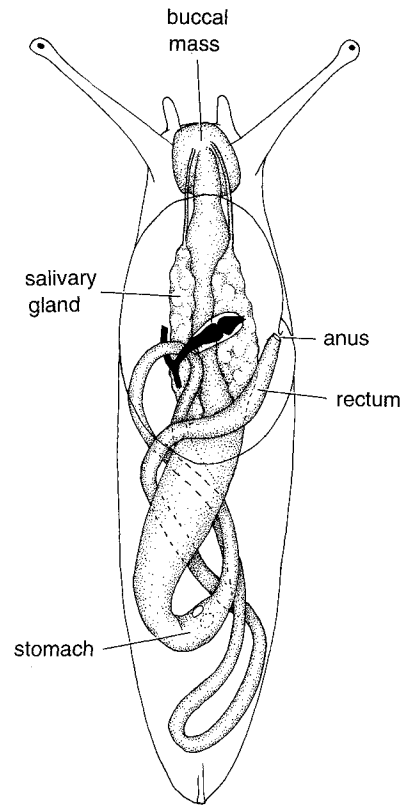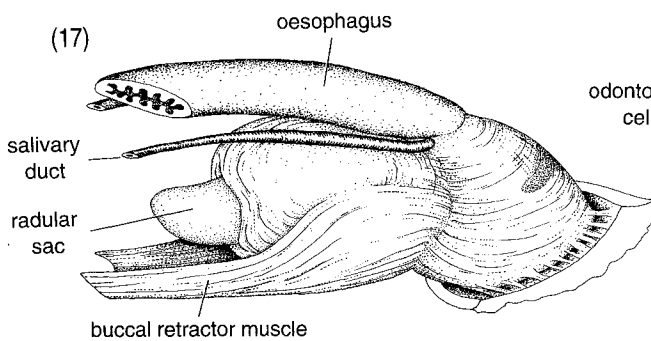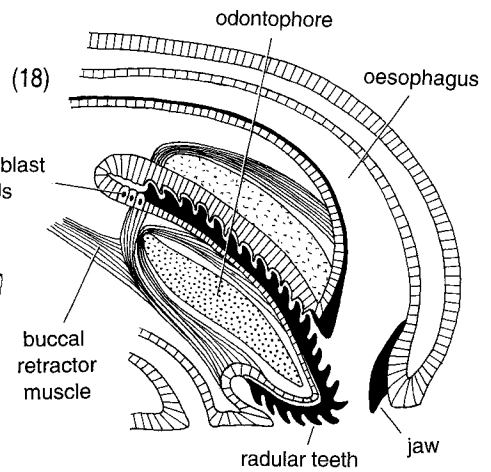
Fig. 15, 16 Generalised layout of digestive system in stylommatophoran snails and slugs. Fig. 17, 18 Stylommatophoran buccal mass: (17) generalised lateral view; (18) schematic longitudinal section, showing features of radula.

(20)

endocone

ectocone

mesocone   basal plate

(19)

(21)

phallus
sheath

phallus

atrium

vagina

epiphallus

vas
deferens

free
oviduct

phallus
retractor
muscle

bursa
copulatrix

prostatic
gland

phallus
appendix

oviducal
gland

talon

albumen
gland

hermaphrodite
duct

ovotestis
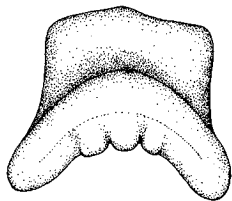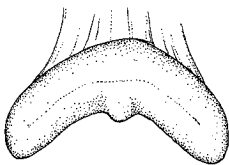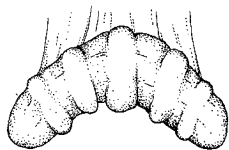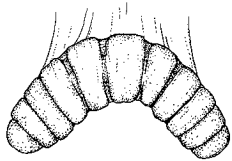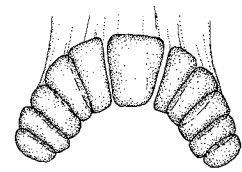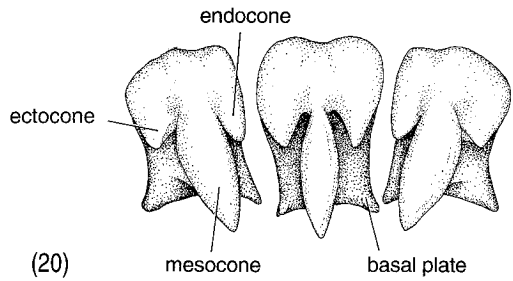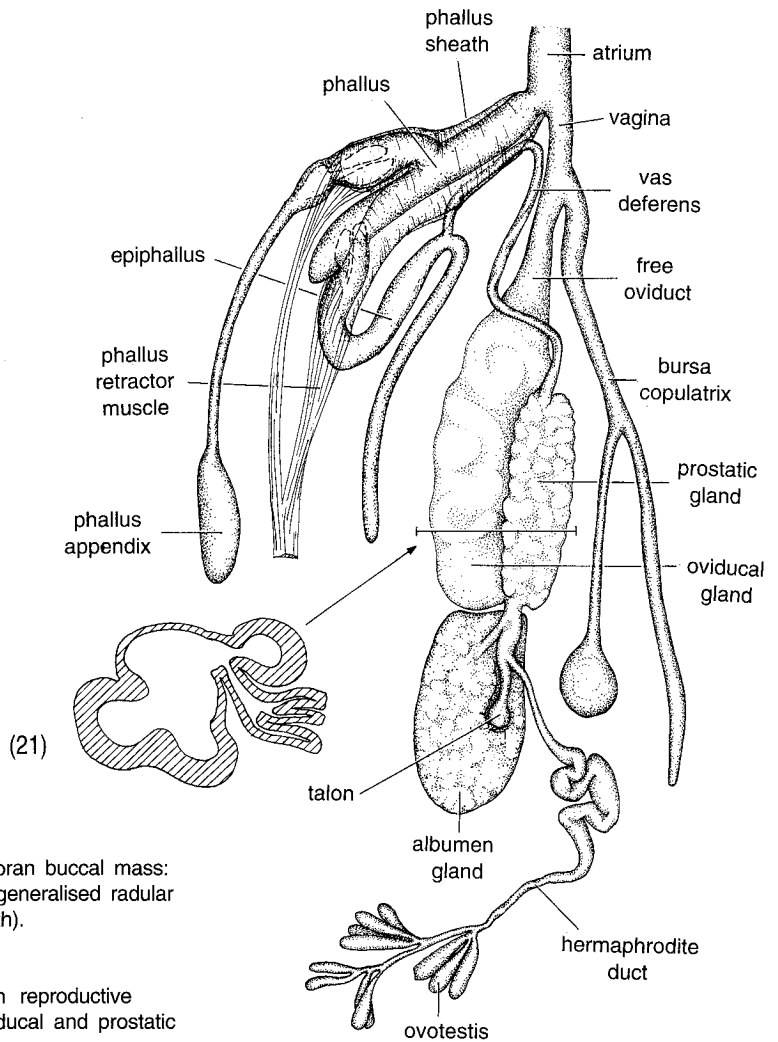
Fig. 19, 20 Features of stylommatophoran buccal mass:
(19) variation in jaw morphology; (21) generalised radular
teeth (central tooth and first lateral teeth).

Fig. 21 Generalised stylommatophoran reproductive
system, with cross-section through oviducal and prostatic
glands.

ocular
retractor
muscle

buccal
retractors

vas
deferens

phallus

bursa
copulatrix
duct

bursa
copulatrix

phallus
retractor
muscle

prostatic
gland

oviducal
gland

albumen
gland

ovotestis

(22)

(23)

cerebral
commissure

cerebral
ganglion

cerebropleural
connective

cerebropedal
connective

pleural
ganglion

pleural-pedal
connective

visceral
ganglion

parietal
ganglion

pedal
ganglion

(24)

Fig. 22, 23 Generalised layout of reproductive system and cephalic part
of columellar retractor muscle system in stylommatophoran snails and slugs.
Fig. 24 Generalised stylommatophoran central nervous system.
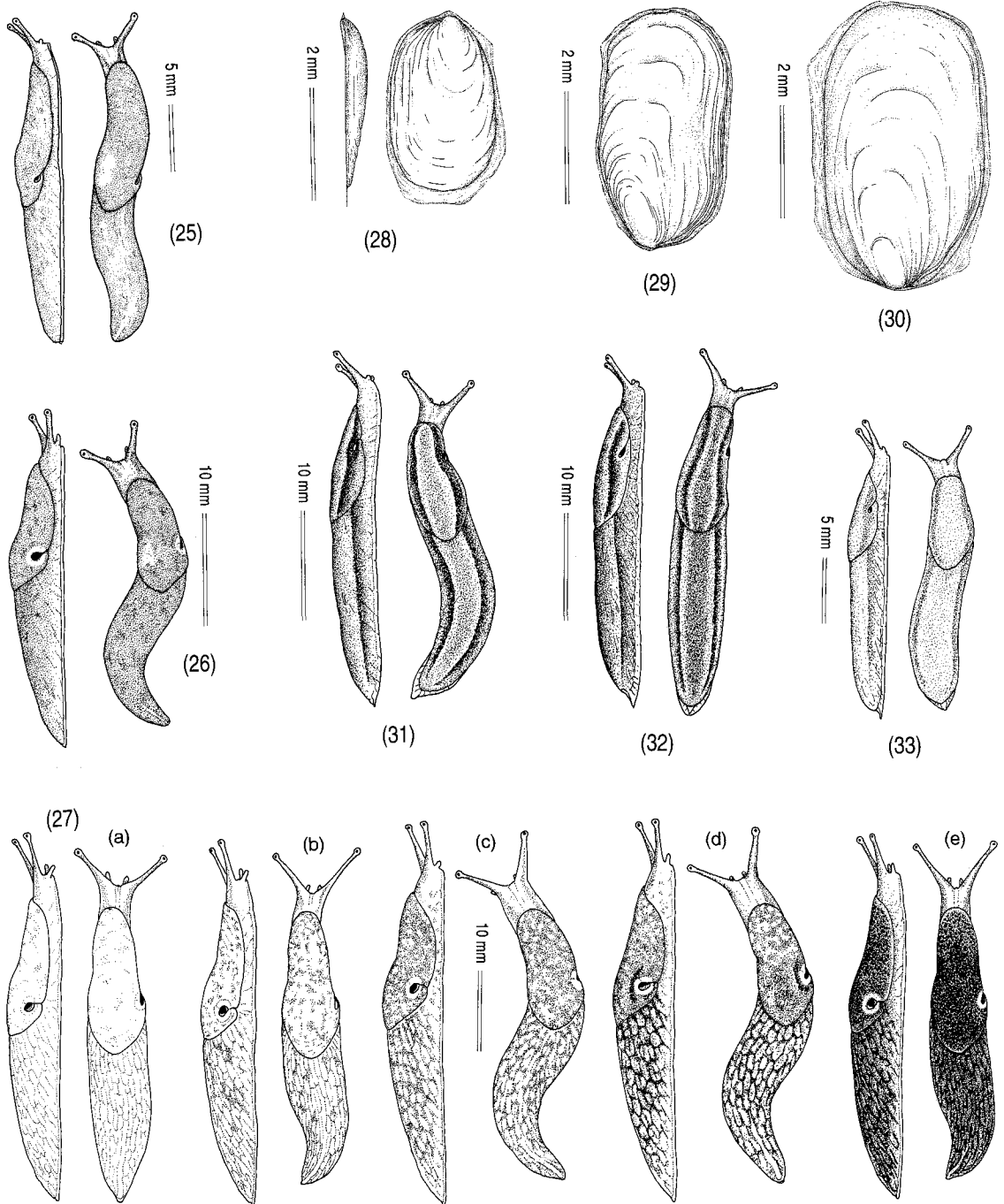
Fig. 25–27 Habitus, lateral and dorsal: (25) *Deroceras laeve*; (26) *D. panormitanum*; (27a–e) *D. reticulatum*, showing variation in body pigmentation. **Fig. 28–30** Shell: (28) *Deroceras laeve*, lateral and dorsal; (29) *D. panormitanum*, dorsal; (30) *D. reticulatum*, dorsal. **Fig. 31–33** Habitus: (31) *Arion distinctus*; (32) *A. hortensis*; (33) *A. intermedius*.

C1 AGRIOLIMACIDAE : *Deroceras laeve*

C2 AGRIOLIMACIDAE : *Deroceras panormitanum*

C3 AGRIOLIMACIDAE : *Deroceras reticulatum*

C4 ARIONIDAE : *Arion distinctus*

C5 ARIONIDAE : *Arion hortensis*

C6 ARIONIDAE : *Arion intermedius*

C7 ARIONIDAE : *Arion intermedius*

C8 COCHLICOPIDAE : *Cochlicopa lubrica*

C9 FERUSSACIIDAE : *Cecilioides acicula*

C10 HELICIDAE : *Cantareus aspersus*

C11 HELICIDAE : *Cantareus aspersus*, juveniles

C12 HYGROMIIDAE : *Candidula intersecta*

C13 HYGROMIIDAE : *Prietocella barbara*

C14 LIMACIDAE : *Lehmannia nyctelia*

C15 LIMACIDAE : *Lehmannia nyctelia*

C16 LIMACIDAE : *Lehmannia valentiana*

C17 LIMACIDAE : *Limacus flavus*

C18 LIMACIDAE : *Limacus flavus*

C19 LIMACIDAE : *Limax maximus*

C20 MILACIDAE : *Milax gagates*

C21 MILACIDAE : *Milax gagates*

C22 MILACIDAE : *Tandonia budapestensis*

C23 MILACIDAE : *Tandonia sowerbyi*

C24 PUPILLIDAE : *Lauria cylindracea*

C25 TESTACELLIDAE : *Testacella haliotidea*

C26 VALLONIIDAE : *Vallonia excentrica*

C27 VERTIGINIDAE : *Vertigo ovata*

C28 ZONITIDAE : *Oxychilus alliarius*

C29 ZONITIDAE : *Oxychilus cellarius*

C30 ZONITIDAE : *Oxychilus draparnaudi*

C31 ZONITIDAE : *Vitrea crystallina*
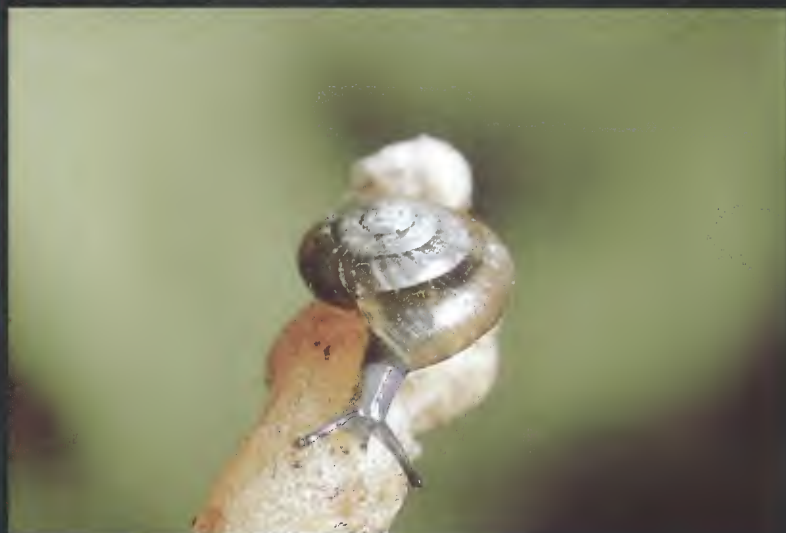
C32 ZONITIDAE : *Zonitoides arboreus*
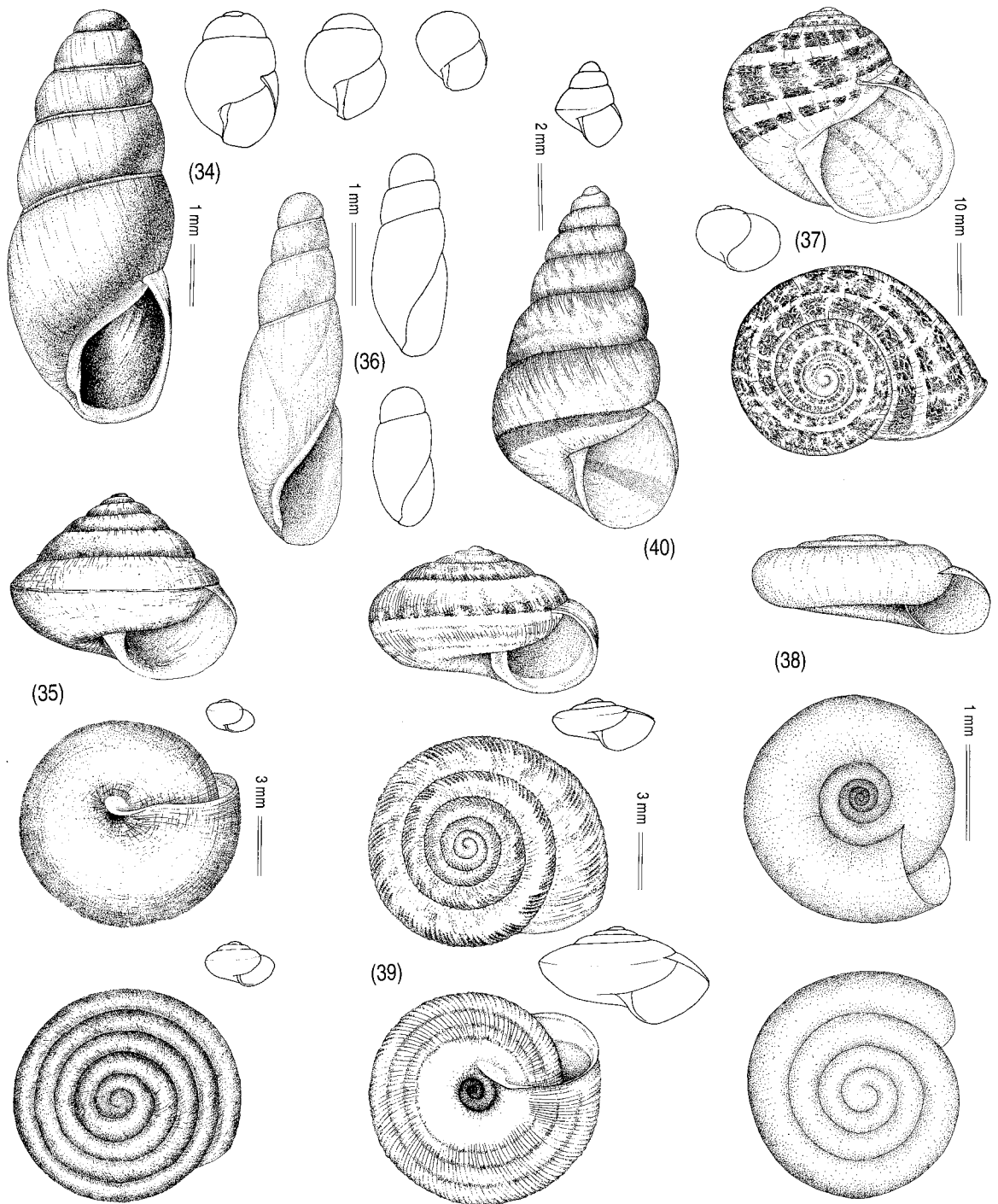
Fig. 34–40 Shell: (34) *Cochlicopa lubrica*, from mature animal and 3 juveniles; (35) *Coneuplecta calculosa*, from mature animal and 2 juveniles; (36) *Cecilioides acicula*, from mature animal and 2 juveniles; (37) *Cantareus aspersus*, from mature animal and a juvenile; (38) *Helicodiscus singleyanus*, from mature animal; (39) *Candidula intersecta*, from mature animal and 2 juveniles; (40) *Prietocella barbara*, from mature animal and a juvenile.
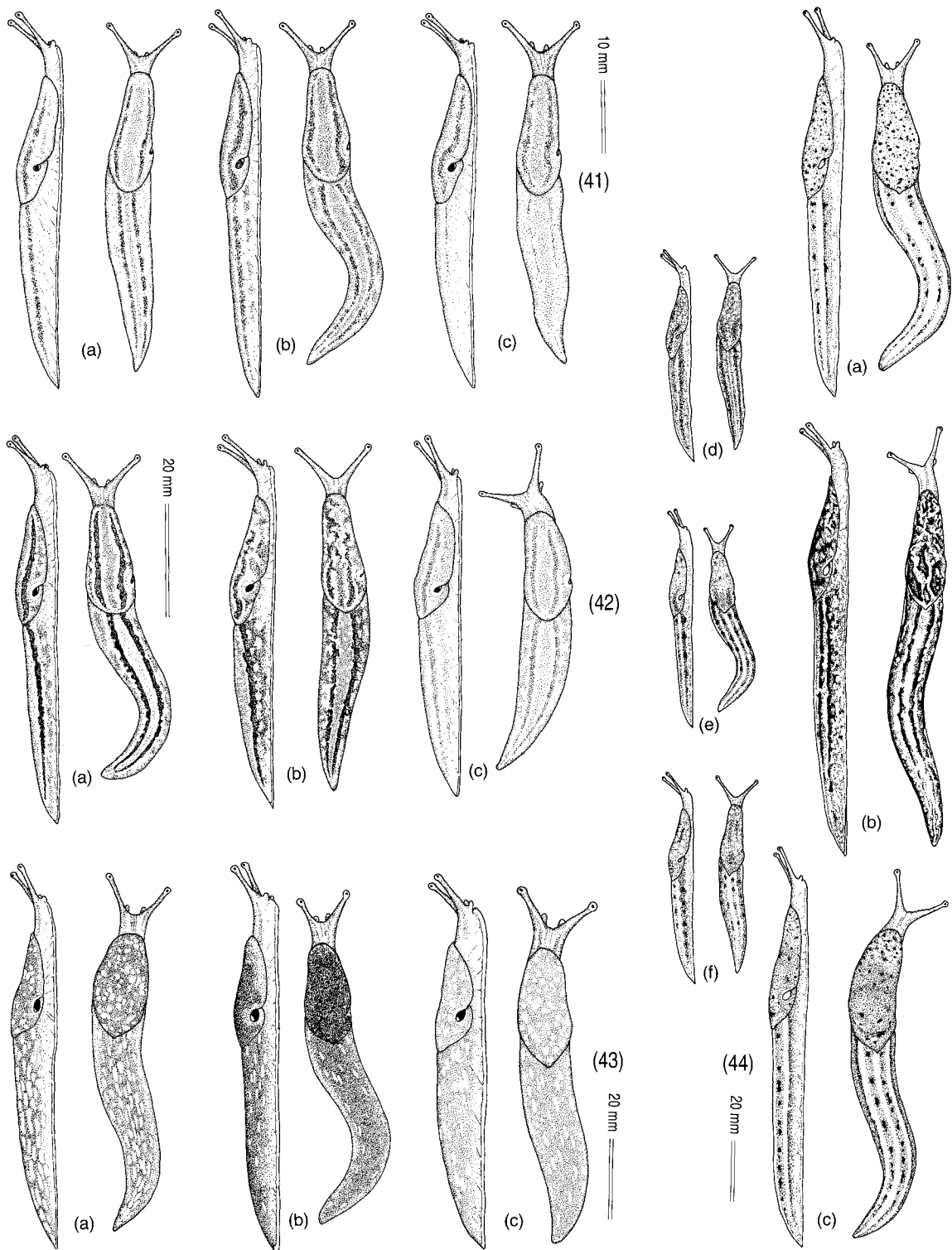
Fig. 41–44 Habitus, showing variation in body pigmentation: (41a–c) *Lehmannia nyctelia*; (42a–c) *L. valentiana*; (43a–c) *Limacus flavus*; (44) *Limax maximus*, adults (a–c) and juveniles (d–f).
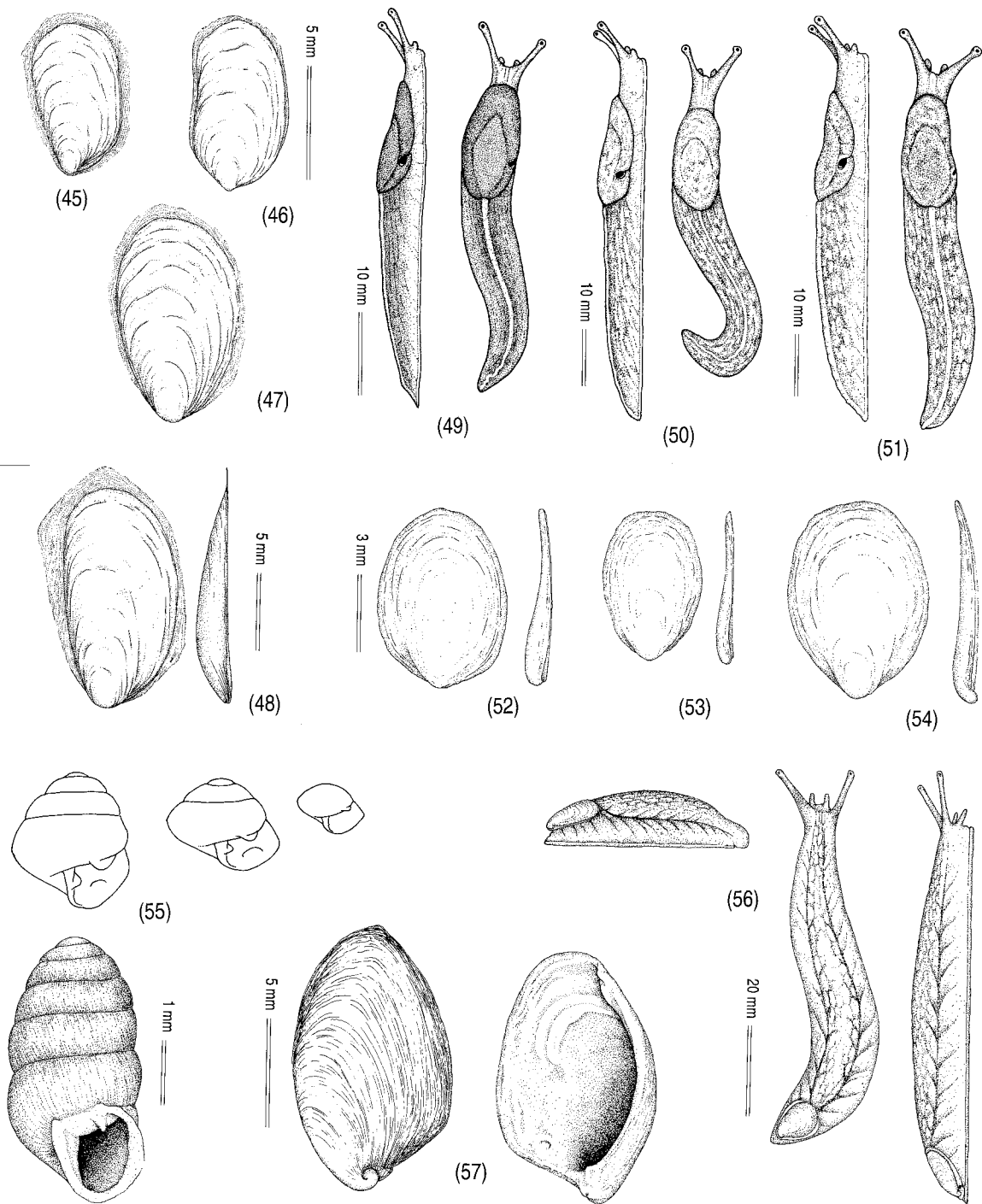
Fig. 45–47 Shell, dorsal: (45) *Lehmannia nyctelia*; (46) *L. valentiana*; (47) *Limacus flavus*. **Fig. 48** *Limax maximus*, shell, dorsal and lateral. **Fig. 49–51** Habitus: (49) *Milax gagates*; (50) *Tandonia budapestensis*; (51) *T. sowerbyi*. **Fig. 52–54** Shell, dorsal and lateral: (52) *Milax gagates*; (53) *Tandonia budapestensis*; (54) *T. sowerbyi*. **Fig. 55** *Lauria cylindracea*, shell, from mature animal and 3 juveniles. **Fig. 56, 57** *Testacella haliotidea*: (56) habitus, dorsal and lateral of extended animal, and lateral of contracted animal; (57) shell, dorsal and ventral.
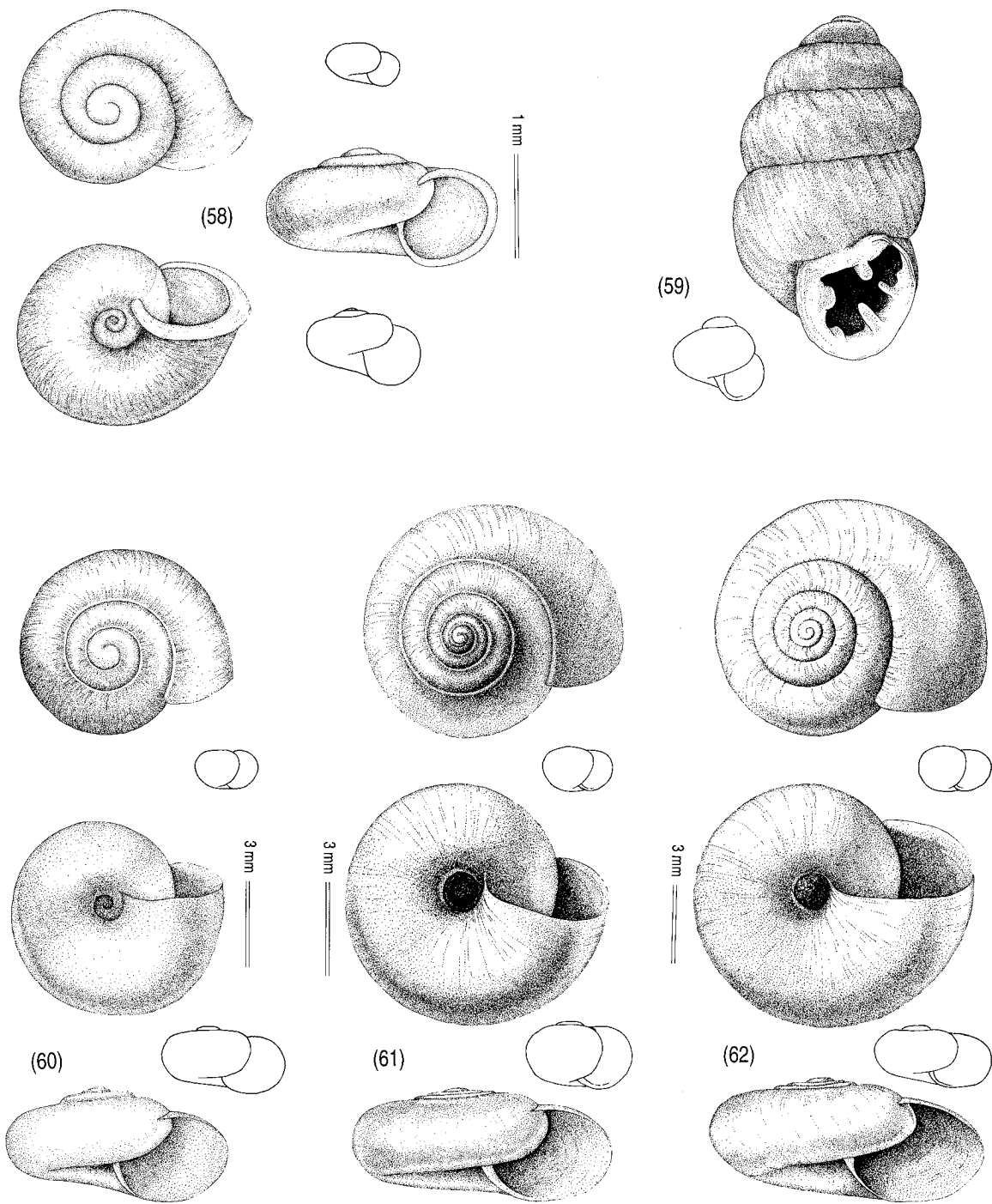
Fig. 58–62 Shell, from mature animal and juveniles: (58) *Vallonia excentrica*; (59) *Vertigo ovata*; (60) *Oxychilus alliarius*; (61) *O. cellarius*; (62) *O. draparnaudi*.
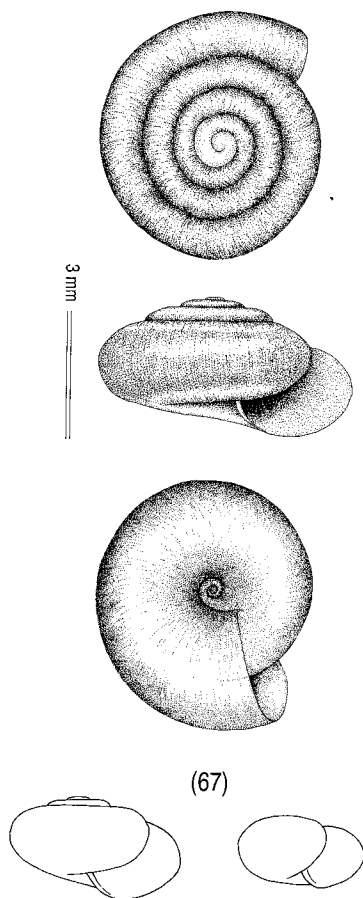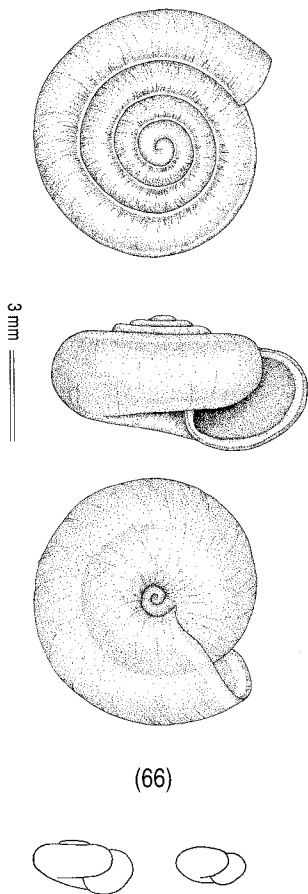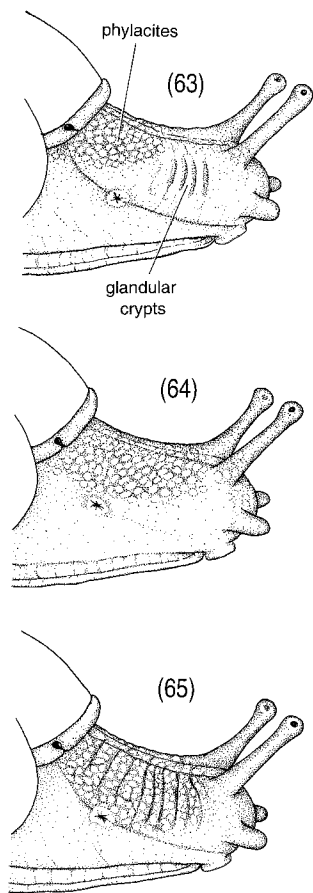
Fig. 63–65 Habitus, anterior lateral, showing phylacites and glandular crypts: (63) *Oxychilus alliarius*; (64) *O. cellarius*; (65) *O. draparnaudi*. **Fig. 66, 67** Shell, from mature animal and 2 juveniles: (66) *Vitrea crystallina*; (67) *Zonitoides arboreus*.
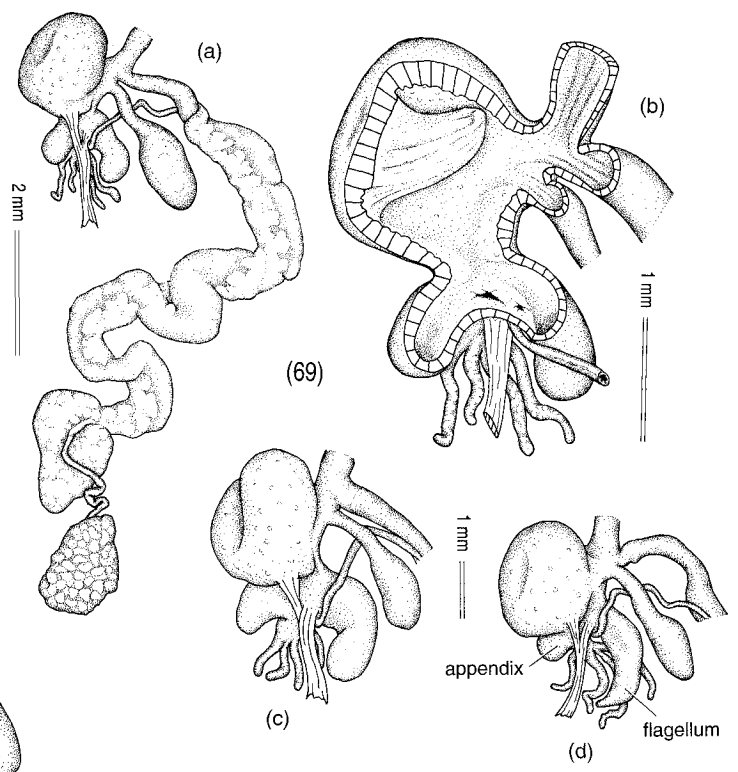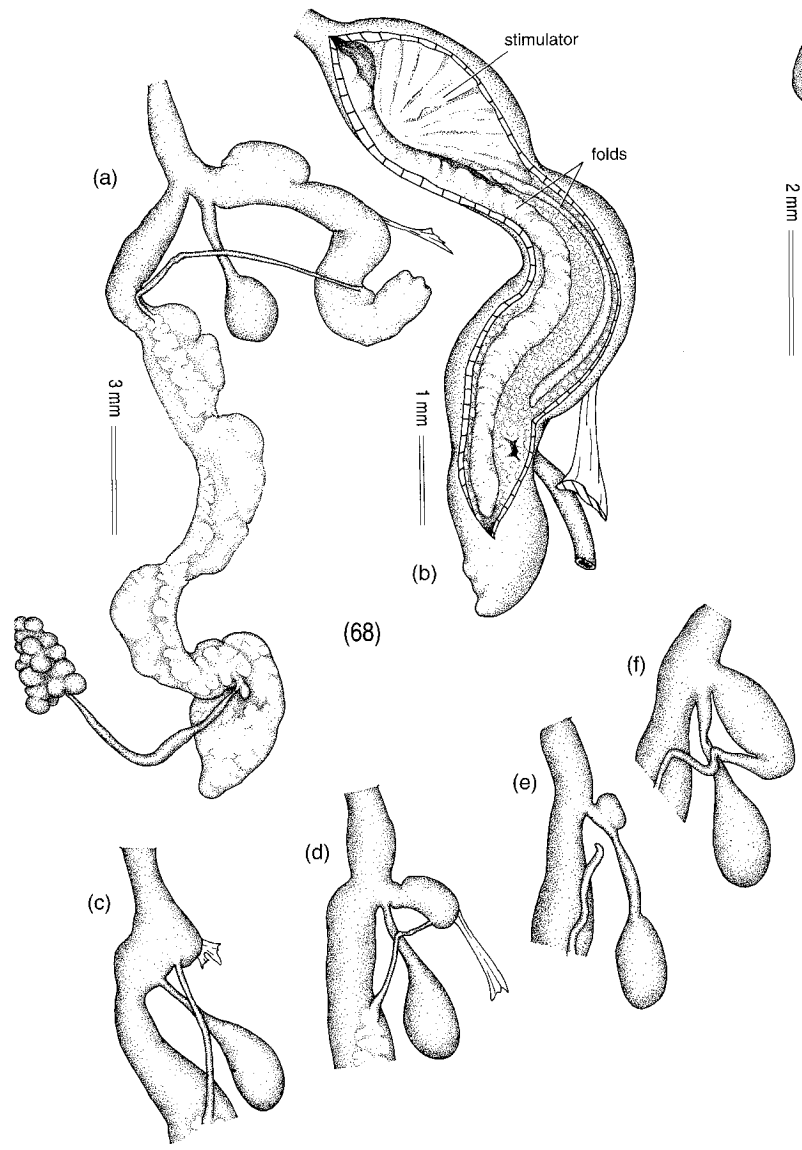
Fig. 68 Reproductive system, *Deroceras laeve*: (a) entire system; (b) phallus of euphallic individual, opened to show longitudinal folds and stimulator; (c–f) distal part of system, showing variation in reduction of male genitalia.

Fig. 69 Reproductive system, *Deroceras panormitanum*: (a) entire system; (b) phallus, opened to show conical stimulator; (c, d) distal part of system, showing variation in form of phallus glands, appendix, and flagellum.

(b)

(c)

(a)

(b)

stimulator

(d)

fold

(e)

verge

phallus
gland

(f)

(70)

(71)

2 mm

0.5 mm

3 mm

2 mm
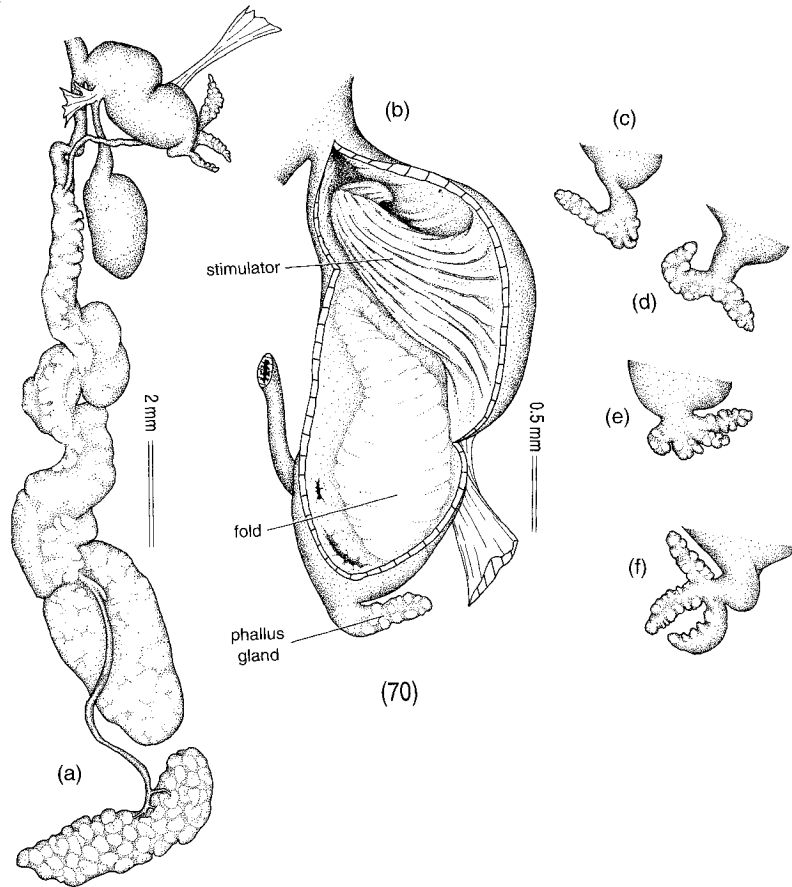
Fig. 70 Reproductive system, *Deroceras reticulatum:* (a) entire system; (b) phallus , opened to show folds and stimulator; (c–f) variation in phallus gland.
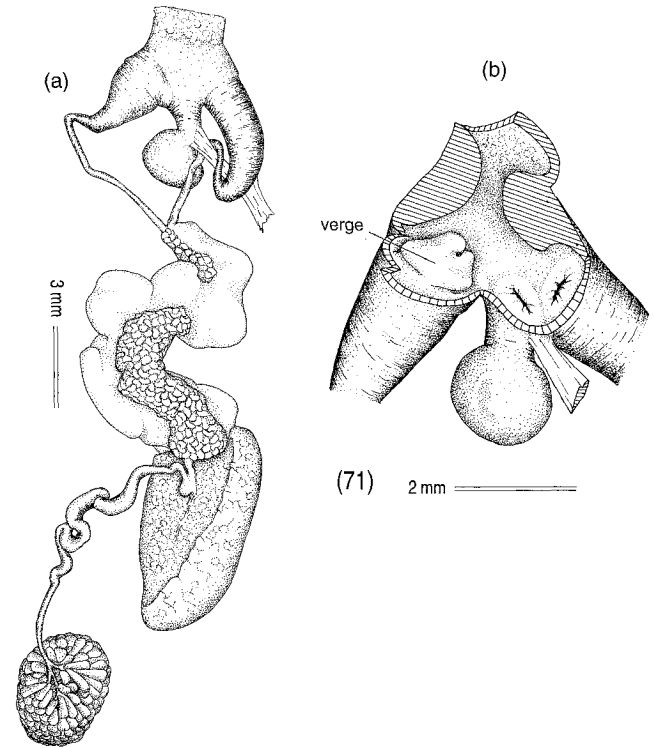
Fig. 71 Reproductive system, *Arion distinctus:* (a) entire system; (b) terminal part of system, opened to show conical verge penetrated by epiphallus and thickened openings of bursa copulatrix and free oviduct.
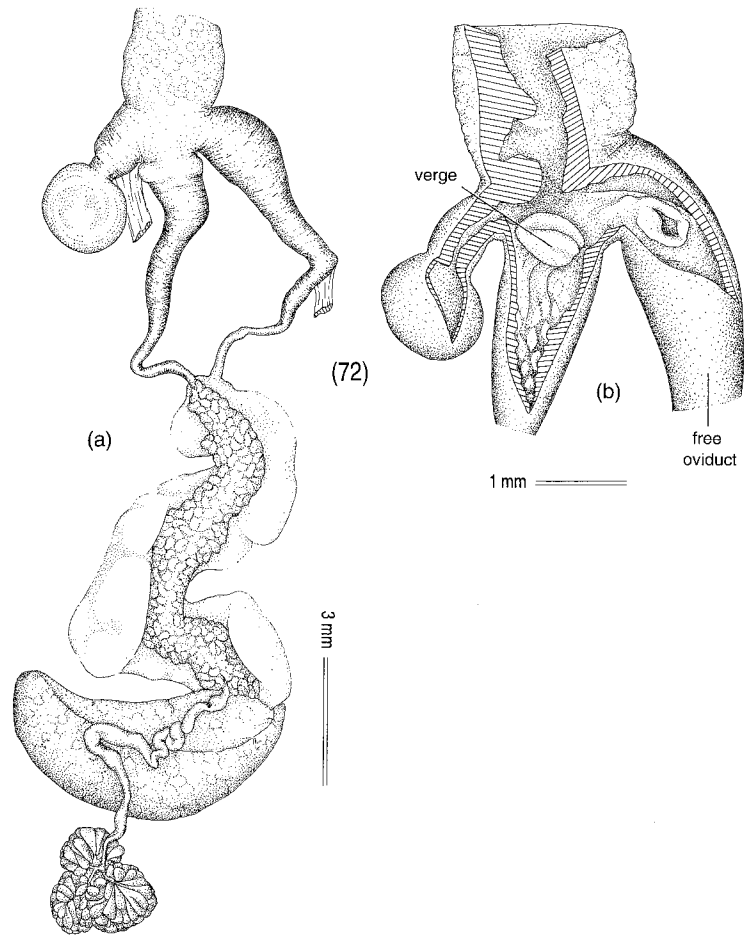
Fig. 72 Reproductive system, *Arion hortensis:* (a) entire system; (b) terminal part of system, opened to show verge overhanging epiphallus opening, and thickened free oviduct opening.
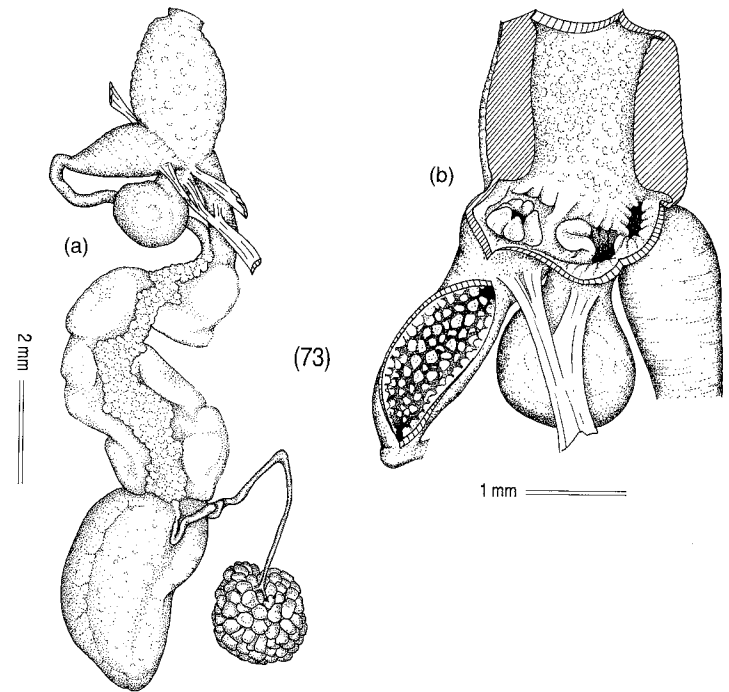
Fig. 73 Reproductive system, *Arion intermedius*: (a) entire system; (b) terminal part of system, opened to show raised, nodulate verge and tongue-like overhang to bursa copulatrix opening.

verge

phallus
appendix

0.2 mm

(74)

(b)

0.5 mm

(a)

-177-

(b)

0.2 mm

(76)

(a)

0.5 mm

1 mm

(75)
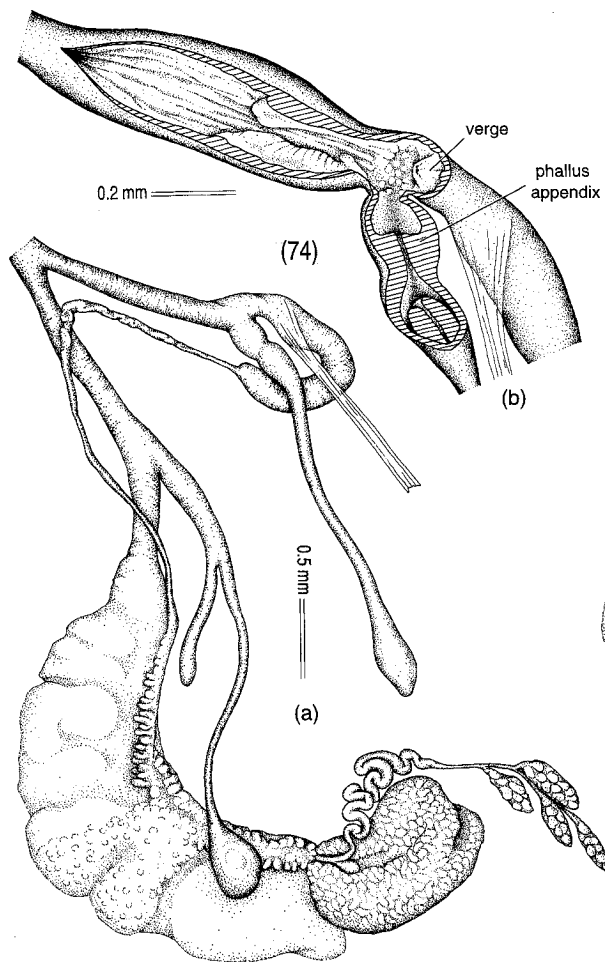
Fig. 74 Reproductive system, *Cochlicopa lubrica*: (a) entire system; (b) phallus, opened to show small vergic papilla, terminal part of phallus appendix, and fleshy stimulatory pads.
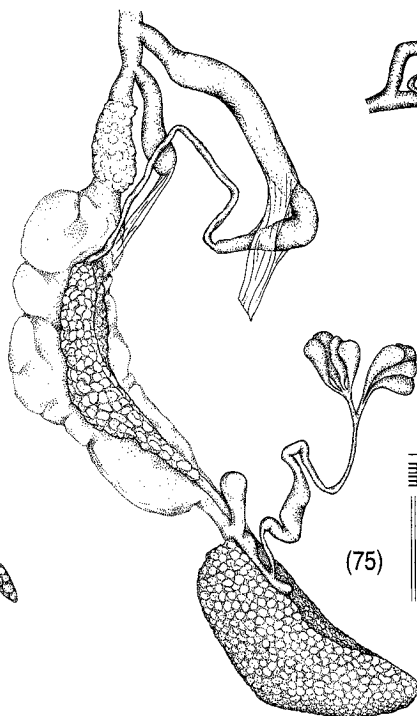
Fig. 75 Reproductive system, *Coneuplecta calculosa.*
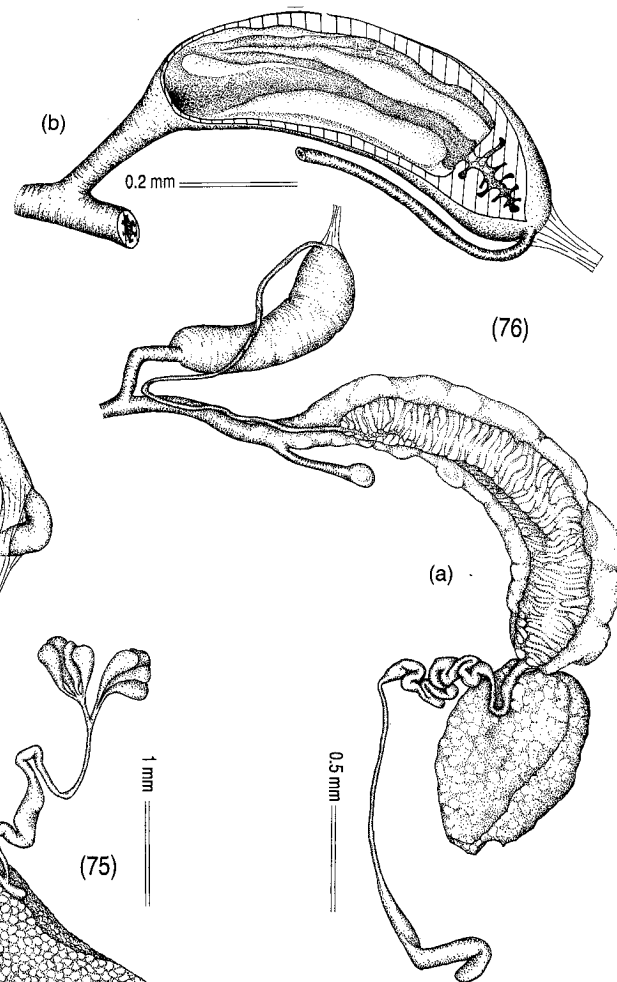
Fig. 76 Reproductive system, *Cecilioides acicula*: (a) entire system; (b) male genitalia, opened to show epiphallus and phallic pilasters.
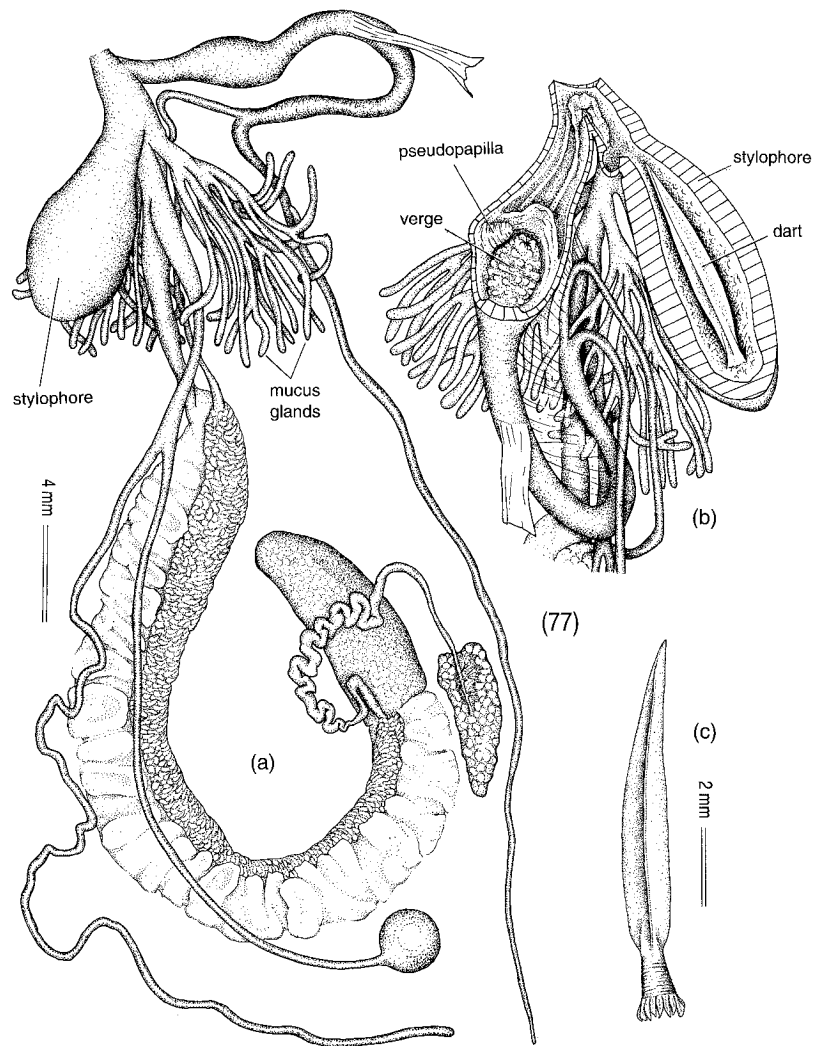
Fig. 77 Reproductive system, *Cantareus aspersus*: (a)entire system; (b) terminal part of system, with phallus opened to show nodulate vergic papilla, pseudopapilla, and stylophore opened to show dart; (c) dart.
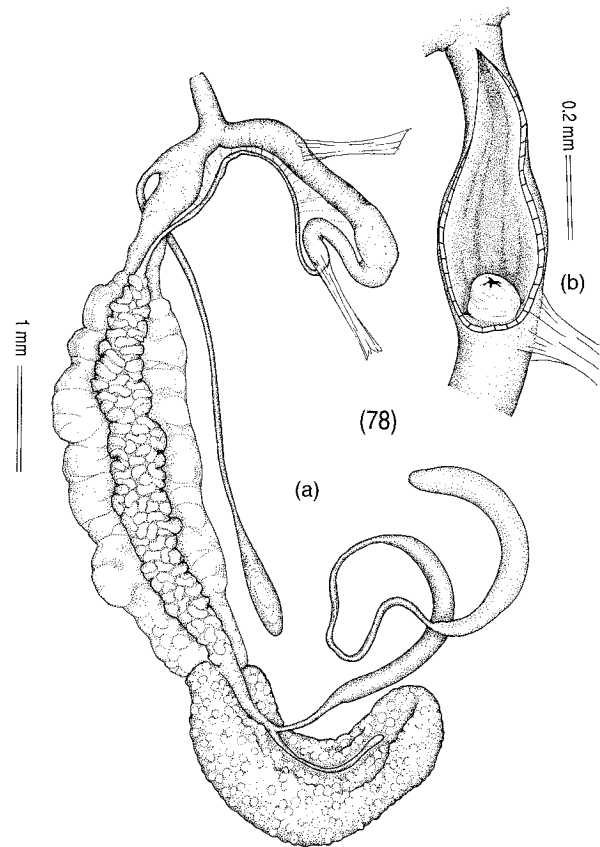
Fig. 78 Reproductive system, *Helicodiscus singleyanus*: (a) entire system; (b) phallus, opened to show vergic papilla and weak longitudinal folds.
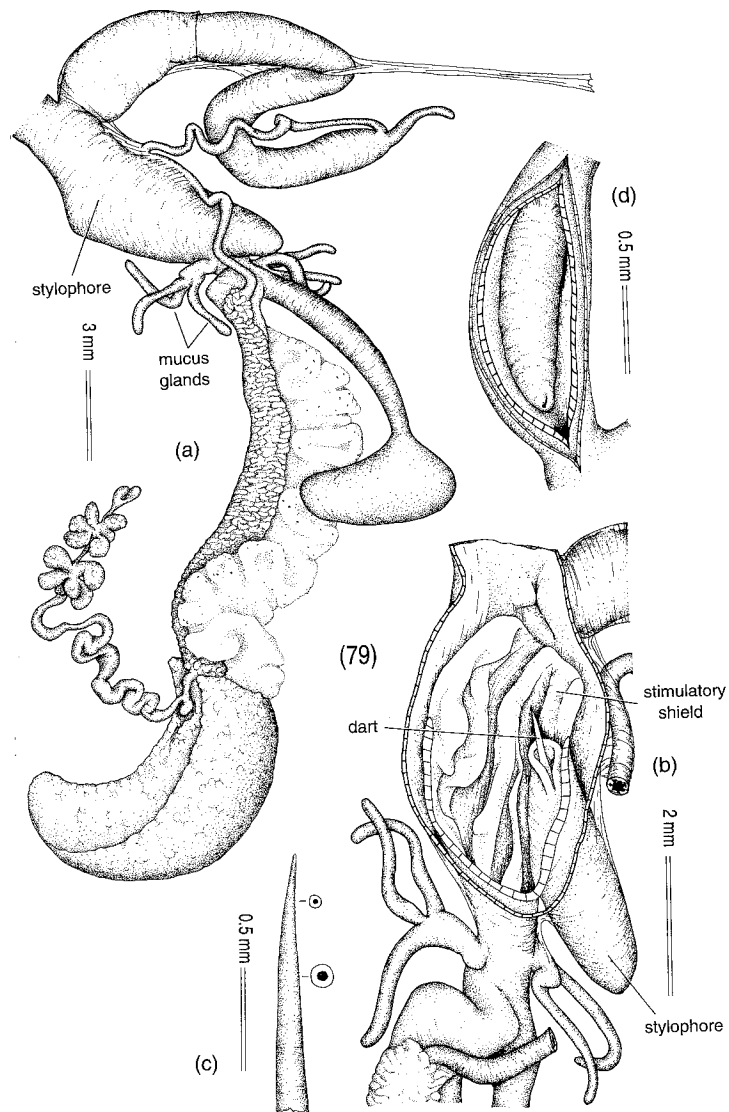
Fig. 79 Reproductive system, *Candidula intersecta*: (a) entire system; (b) terminal female genitalia, opened to show dart in stylophore and stimulatory shield on vaginal walls; (c) dart; (d) phallus, opened to show elongate epiphallic papilla.
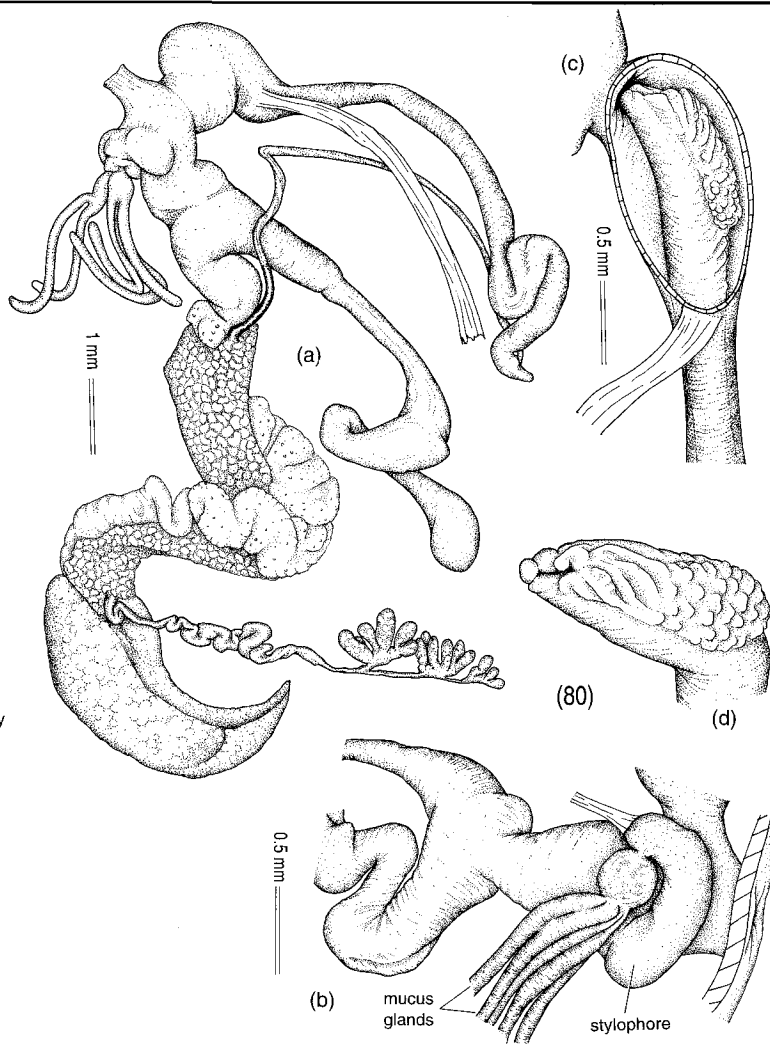
Fig. 80 Reproductive system, *Prietocella barbara* : (a) entire system; (b) terminal part of female genitalia, showing stylophore and mucus glands; (c) phallus, opened to show epiphallic papilla; (d) epiphallic papilla from phallus, showing nodulate surface.

talon

(c)

(a)

(82)

(b)

appendix

(81)

(b)

(a)

(a)

(b)

(83)

(b)
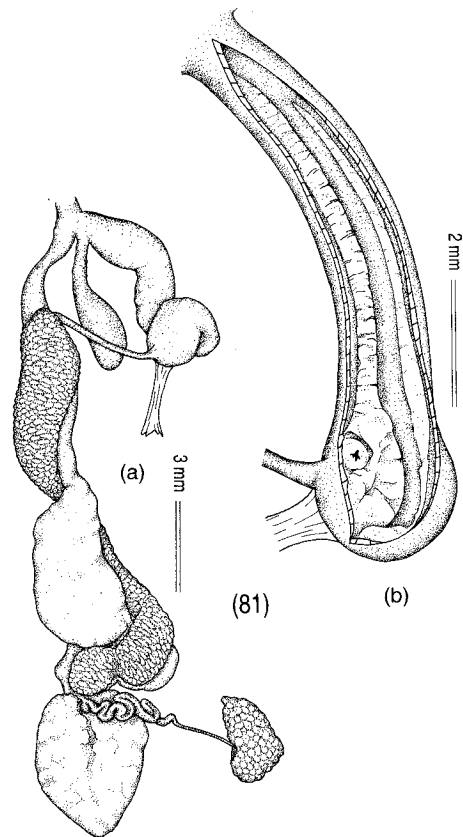
Fig. 81 Reproductive system, *Lehmannia nyctelia*: (a) entire system; (b) phallus, opened to show longitudinal folds.
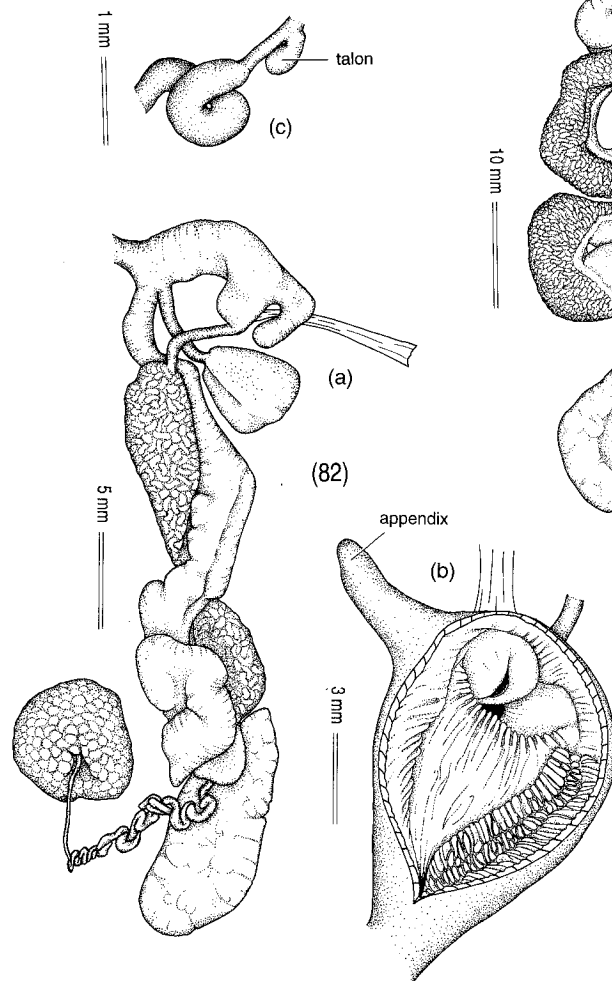
Fig. 82 Reproductive system, *Lehmannia valentiana*: (a) entire system; (b) phallus, opened to show internal folds; (c) terminal part of hermaphrodite duct, with talon.
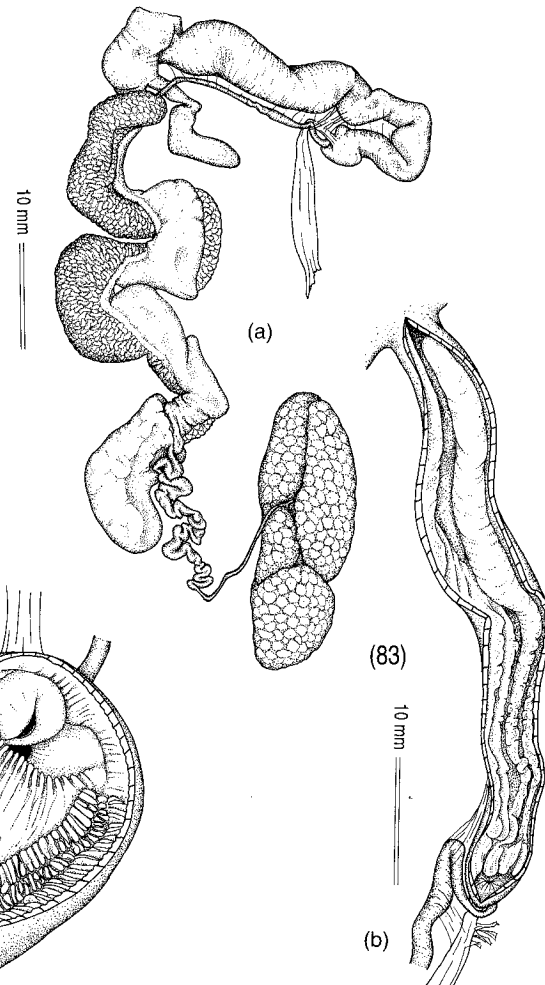
Fig. 83 Reproductive system, *Limacus flavus*: (a) entire system; (b) phallus, opened to show longitudinal folds.

accessory
atrial
glands

atrial
stimulator

5 mm

5 mm

3 mm

5 mm

(a)

(a)

(a)

(b)

(85)

(a)

(b)

(84)

(86)

(b)

2 mm

(b)

3 mm
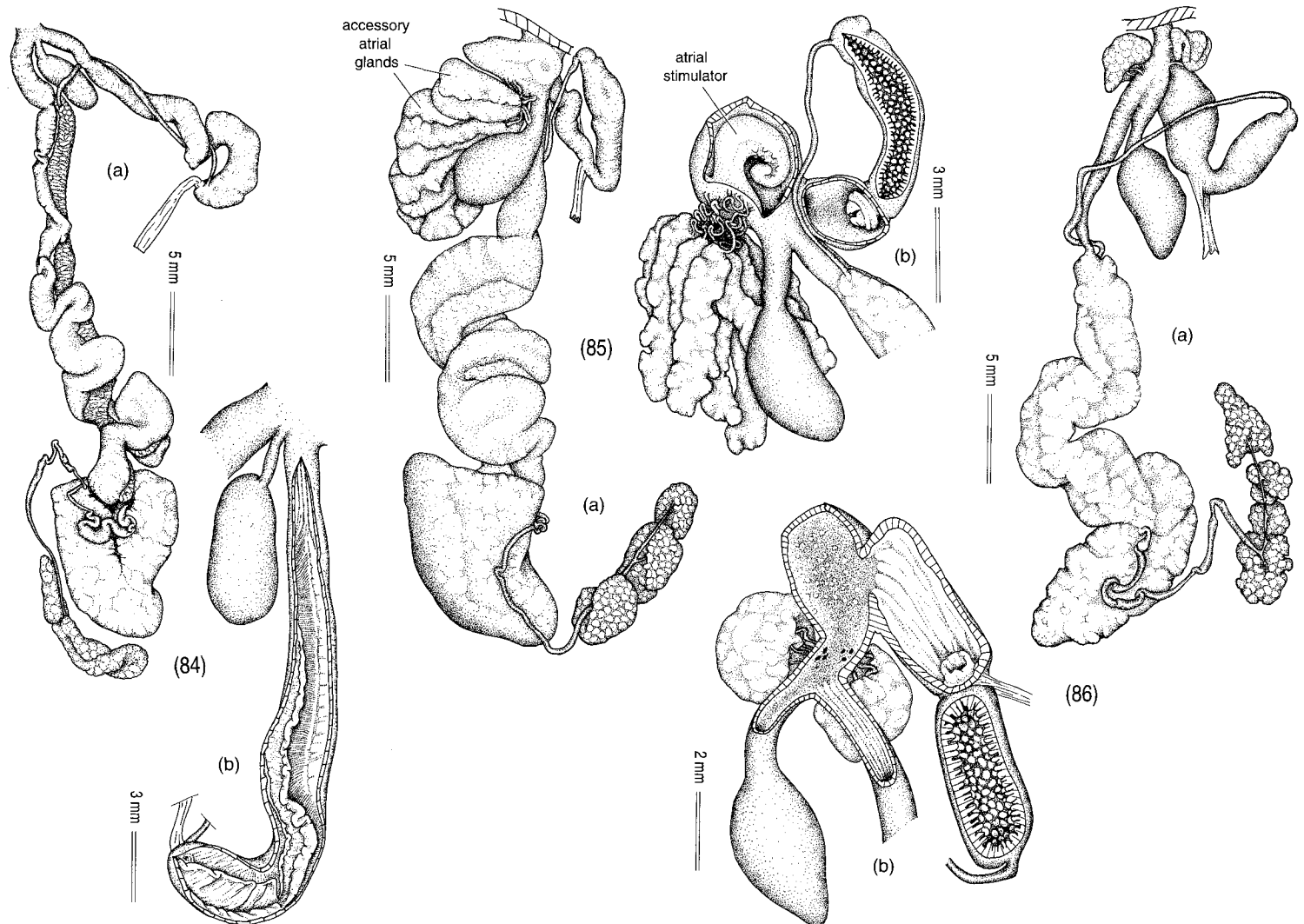
Fig. 84 Reproductive system, *Limax maximus*: (a) entire system;
(b) phallus, opened to show longitudinal folds.
Fig. 85 Reproductive system, *Milax gagates*: (a) entire system; (b) terminal
part of system, with epiphallus opened to show finely papillate walls, phallus
opened to show epiphallic papilla, and atrium opened to show stimulator.

Fig. 86 Reproductive system, *Tandonia budapestensis*: (a) entire system;
(b) terminal part of system, with epiphallus opened to show finely papillate
walls, phallus opened to show epiphallic papilla, and vagina opened to show
entry of accessory glands.
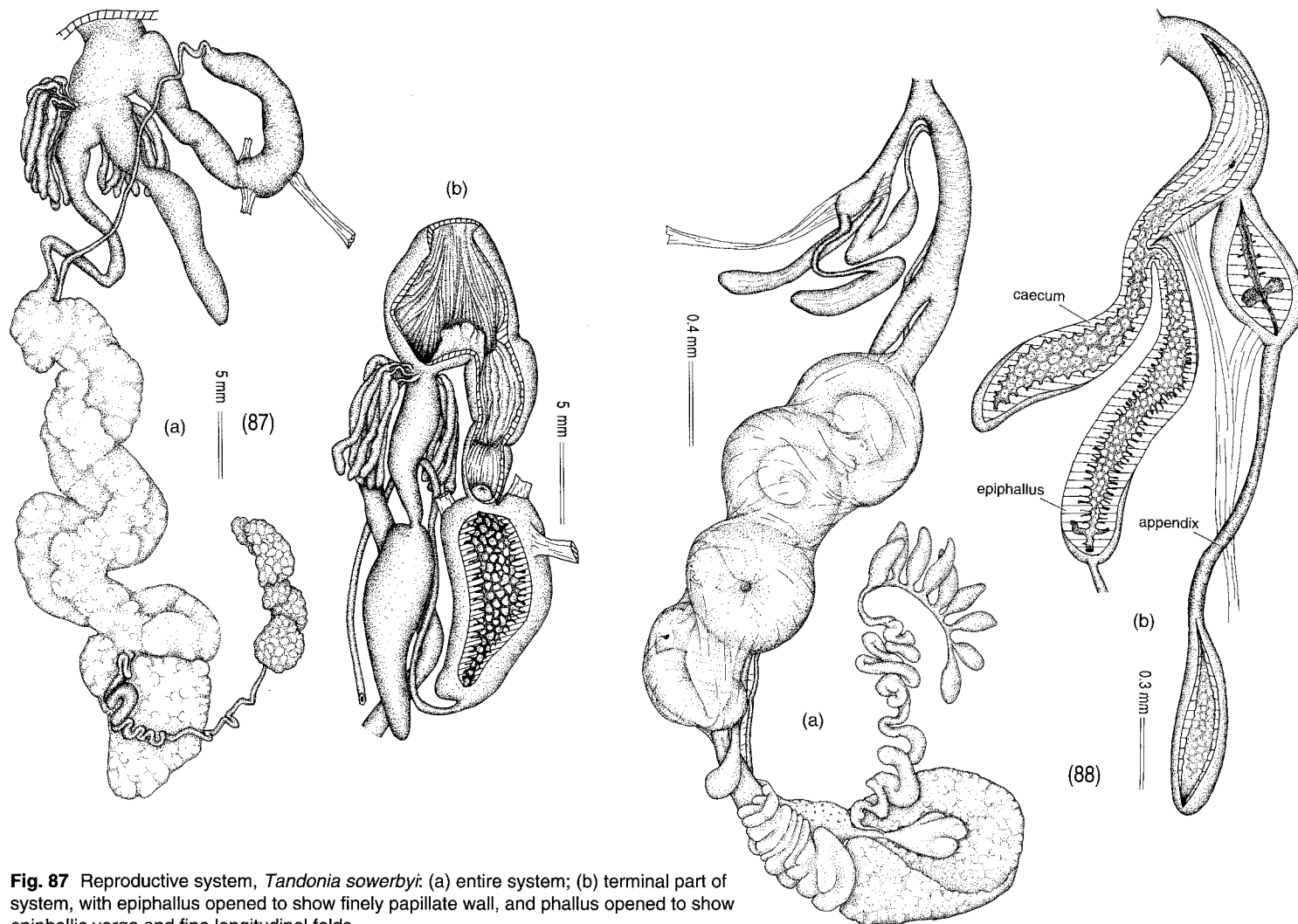
Fig. 87 Reproductive system, *Tandonia sowerbyi*: (a) entire system; (b) terminal part of system, with epiphallus opened to show finely papillate wall, and phallus opened to show epiphallic verge and fine longitudinal folds.

Fig. 88 Reproductive system, *Lauria cylindracea*: (a) entire system; (b) terminal part of male genitalia, with epiphallus opened to show finely papillate lumen, and phallus opened to show caecum with spinate papillae and thick wall of bulbous terminus of appendix.

(c)

(90)

(89)

3 mm

(b)

0.5 mm

(a)
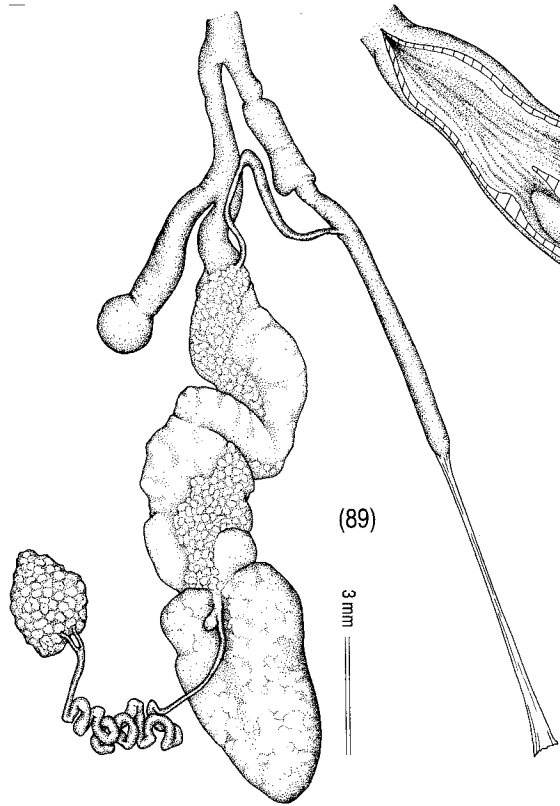
Fig. 89 Reproductive system, *Testacella haliotidea.*
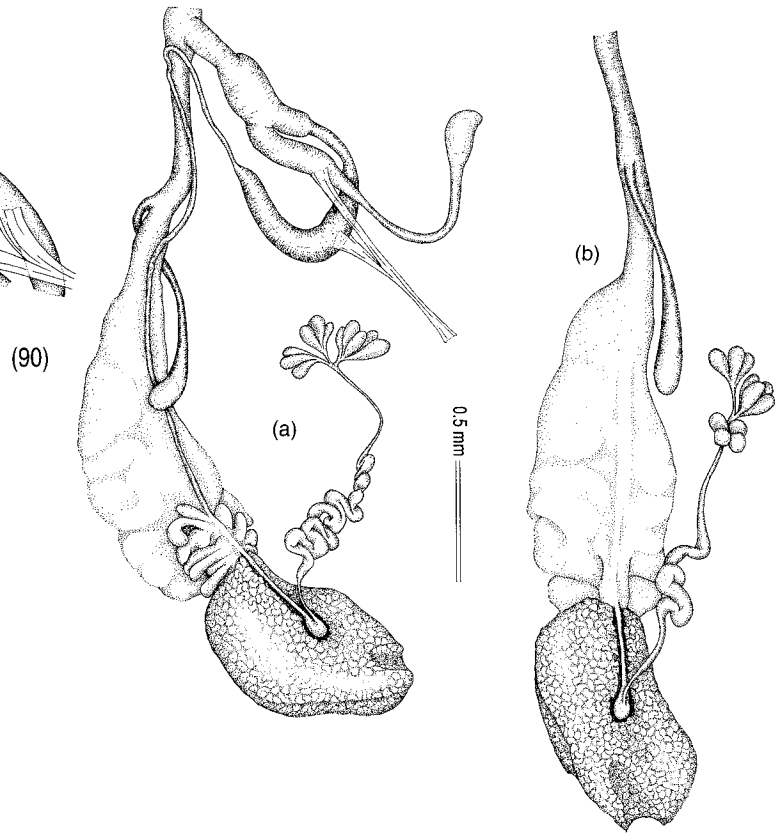
Fig. 90 Reproductive system, *Vallonia excentrica*: (a) entire system of euphallic individual; (b) entire system of aphallic individual; (c) phallus, opened to show epiphallic papilla.
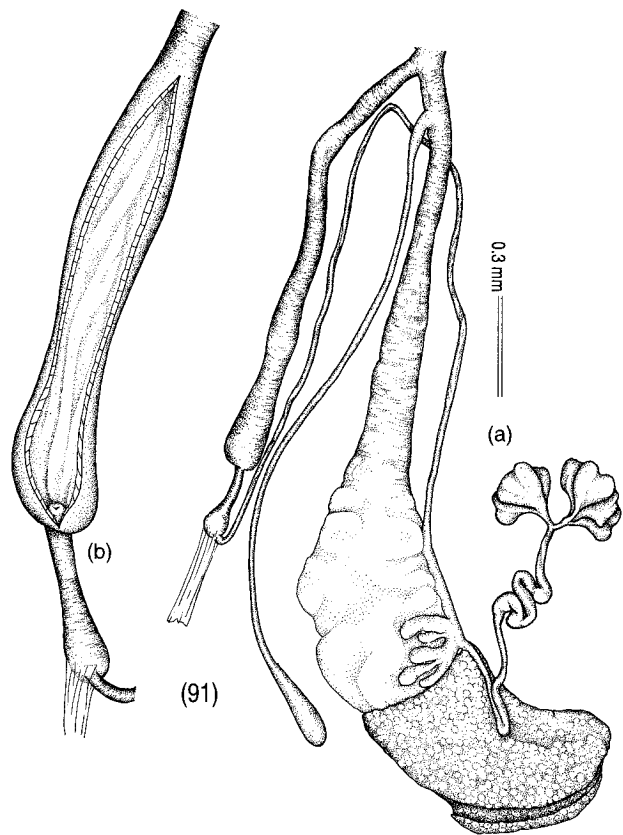
Fig. 91 Reproductive system, *Vertigo ovata*: (a) entire system; (b) phallus, opened to show small epiphallic papilla and low longitudinal folds.
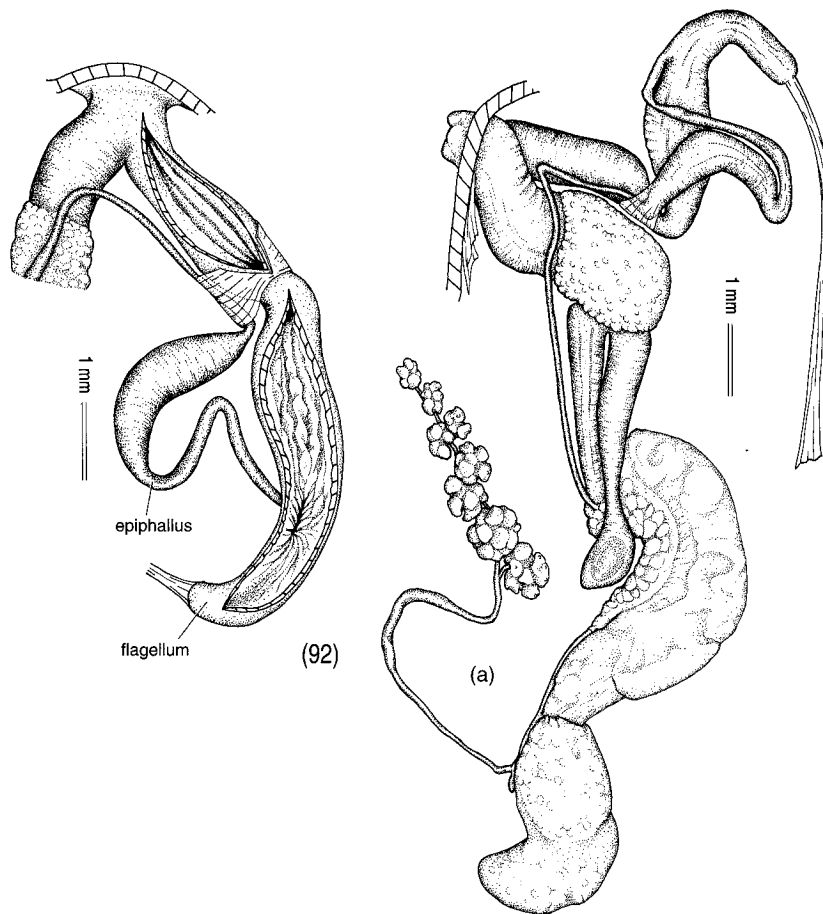
Fig. 92 Reproductive system, *Oxychilus alliarius*: (a) entire system; (b) phallus, opened to show flagellum above entry of epiphallus, weakly papillate folds in proximal part, and rather smooth folds in distal part.
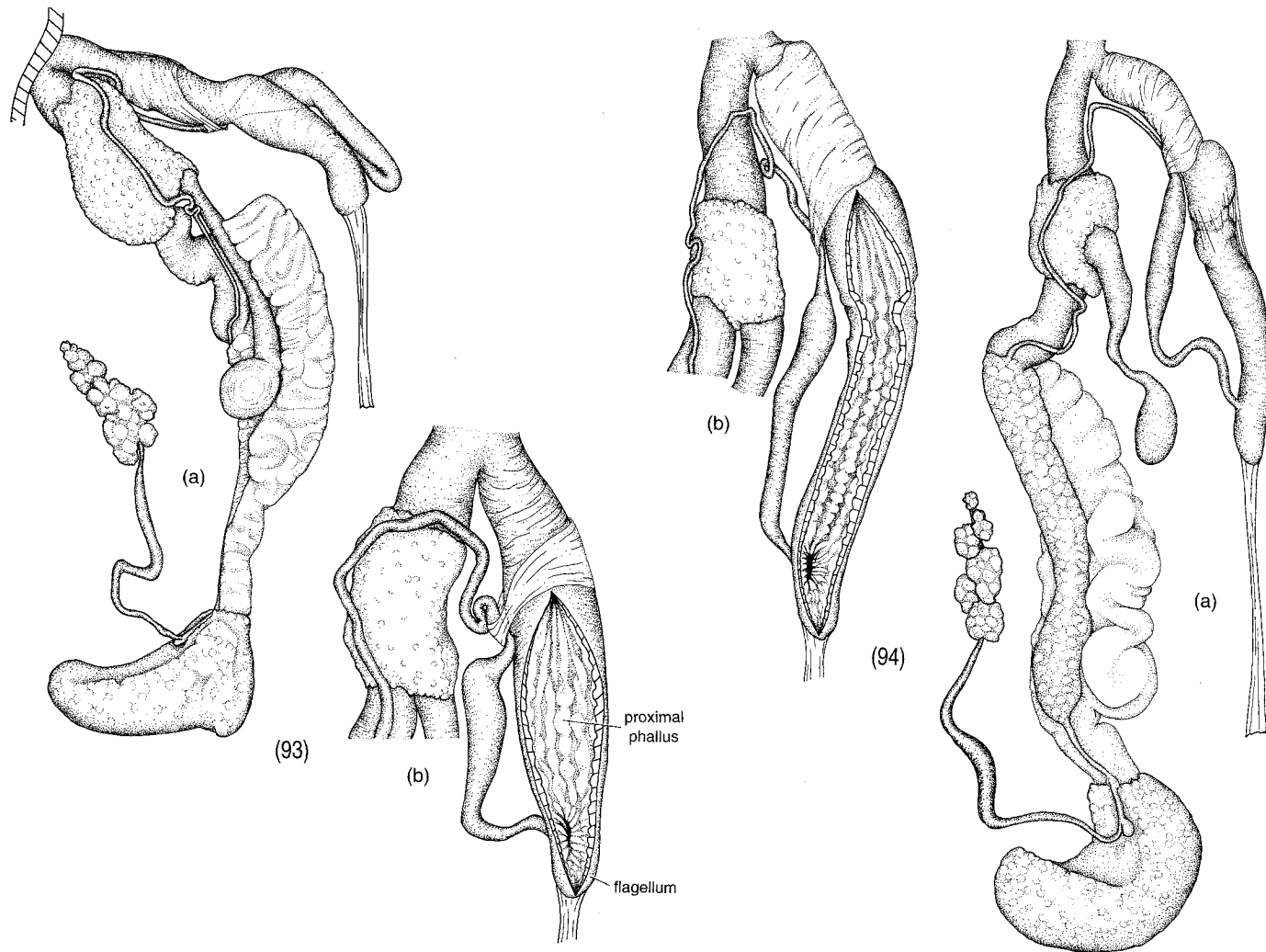
Fig. 93 Reproductive system, *Oxychilus cellarius*: (a) entire system; (b) terminal part of system, with phallus opened to show very short flagellum above entry of epiphallus, and longitudinal folds in proximal part bearing large papillae.

Fig. 94 Reproductive system, *Oxychilus draparnaudi*: (a) entire system; (b) terminal part of system, with phallus opened to show very short flagellum above entry of epiphallus, papillate folds in proximal part, and weakly papillate or smooth folds in distal part.

Labels within figures: stimulator, pseudopapilla, (95), (a), (b); (b), epiphallic papilla, calcareous plate, coronary gland, dart, dart papilla, (96), (c), (a); (97), (98), (99); scale bars 1 mm, 0.5 mm.
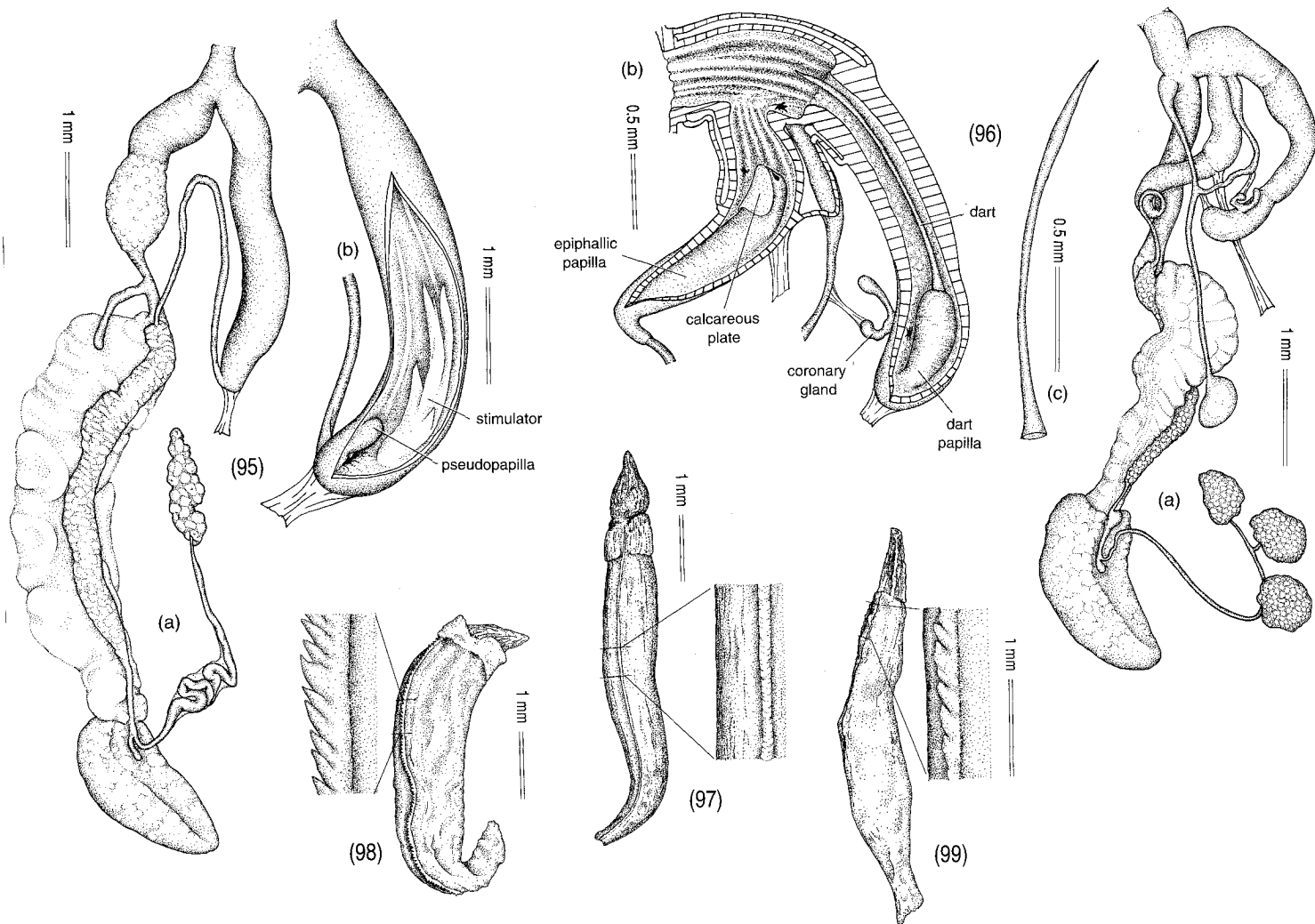
Fig. 95 Reproductive system, *Vitrea crystallina*: (a) entire system; (b) phallus, opened to show pseudopapilla near entry of vas deferens, and frilled stimulator pad. **Fig. 96** Reproductive system, *Zonitoides arboreus*: (a) entire system; (b) male genitalia, opened to show large epiphallic papilla invested with a calcareous plate, and dart sac containing dart; (c) dart. **Fig. 97–99** Spermatophores: (97) *Arion distinctus*; (98) *A. hortensis*; (99) *A. intermedius*.
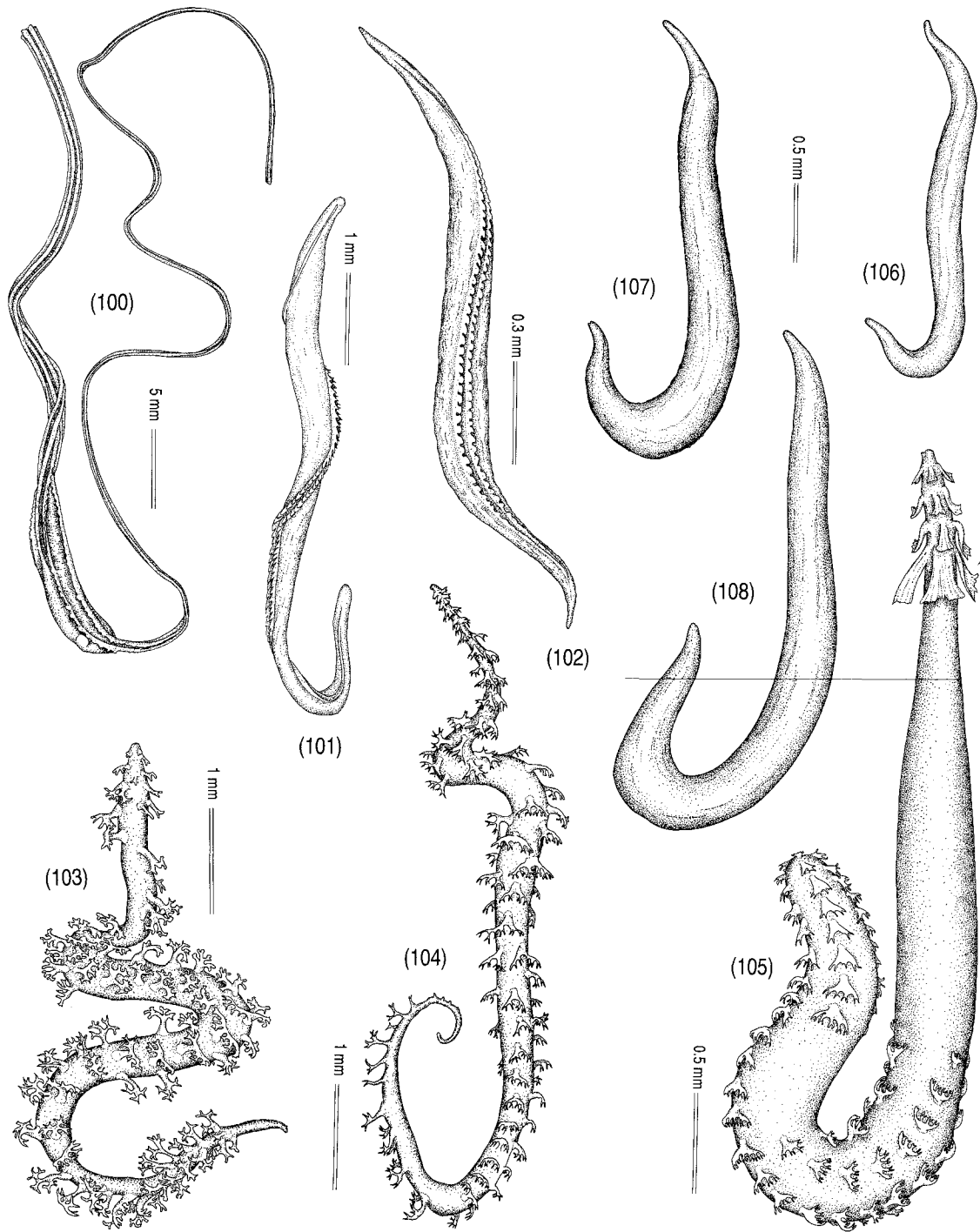
Fig. 100–108 Spermatophores: (100) *Cantareus aspersus*; (101) *Candidula intersecta*; (102) *Prietocella barbara*; (103) *Milax gagates*; (104) *Tandonia budapestensis*; (105) *T. sowerbyi*; (106) *Oxychilus alliarius*; (107) *O. cellarius*; (108) *O. draparnaudi*.
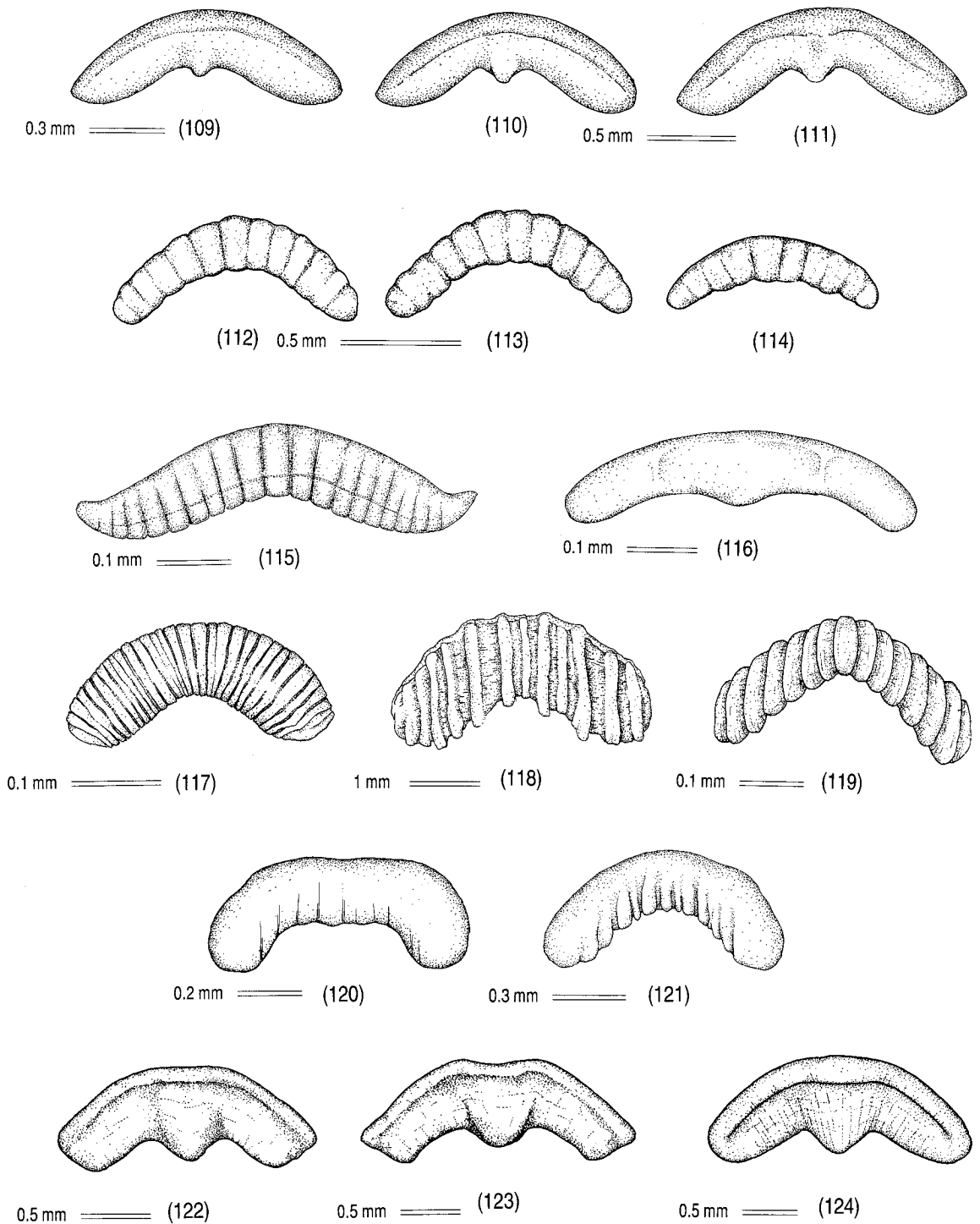
Fig. 109–124 Jaws: (109) *Deroceras laeve*; (110) *D. panormitanum*; (111) *D. reticulatum*; (112) *Arion distinctus*; (113) *A. hortensis*; (114) *A. intermedius*; (115) *Cochlicopa lubrica*; (116) *Coneuplecta calculosa*; (117) *Cecilioides acicula*; (118) *Cantareus aspersus*; (119) *Helicodiscus singleyanus*; (120) *Candidula intersecta*; (121) *Prietocella barbara*; (122) *Lehmannia nyctelia*; (123) *L. valentiana*; (124) *Limacus flavus*.
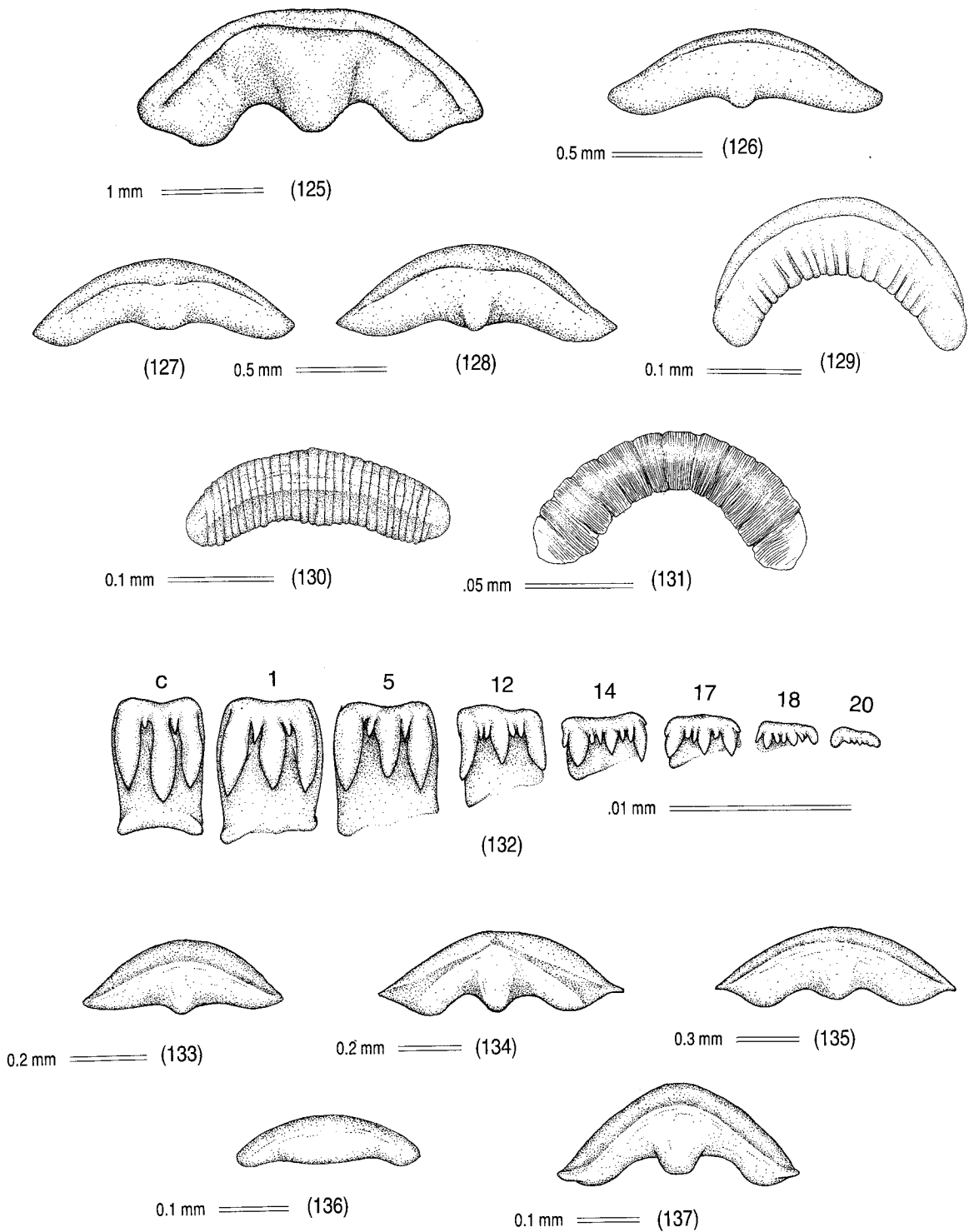
Fig. 125–137 Jaws: (125) *Limax maximus*; (126) *Milax gagates*; (127) *Tandonia budapestensis*; (128) *T. sowerbyi*; (129) *Lauria cylindracea*; (130) *Vallonia excentrica*; (131) *Vertigo ovata* with (132) radular teeth; (133) *Oxychilus alliarius*; (134) *O. cellarius*; (135) *O. draparnaudi*; (136) *Vitrea crystallina*; (137) *Zonitoides arboreus*.
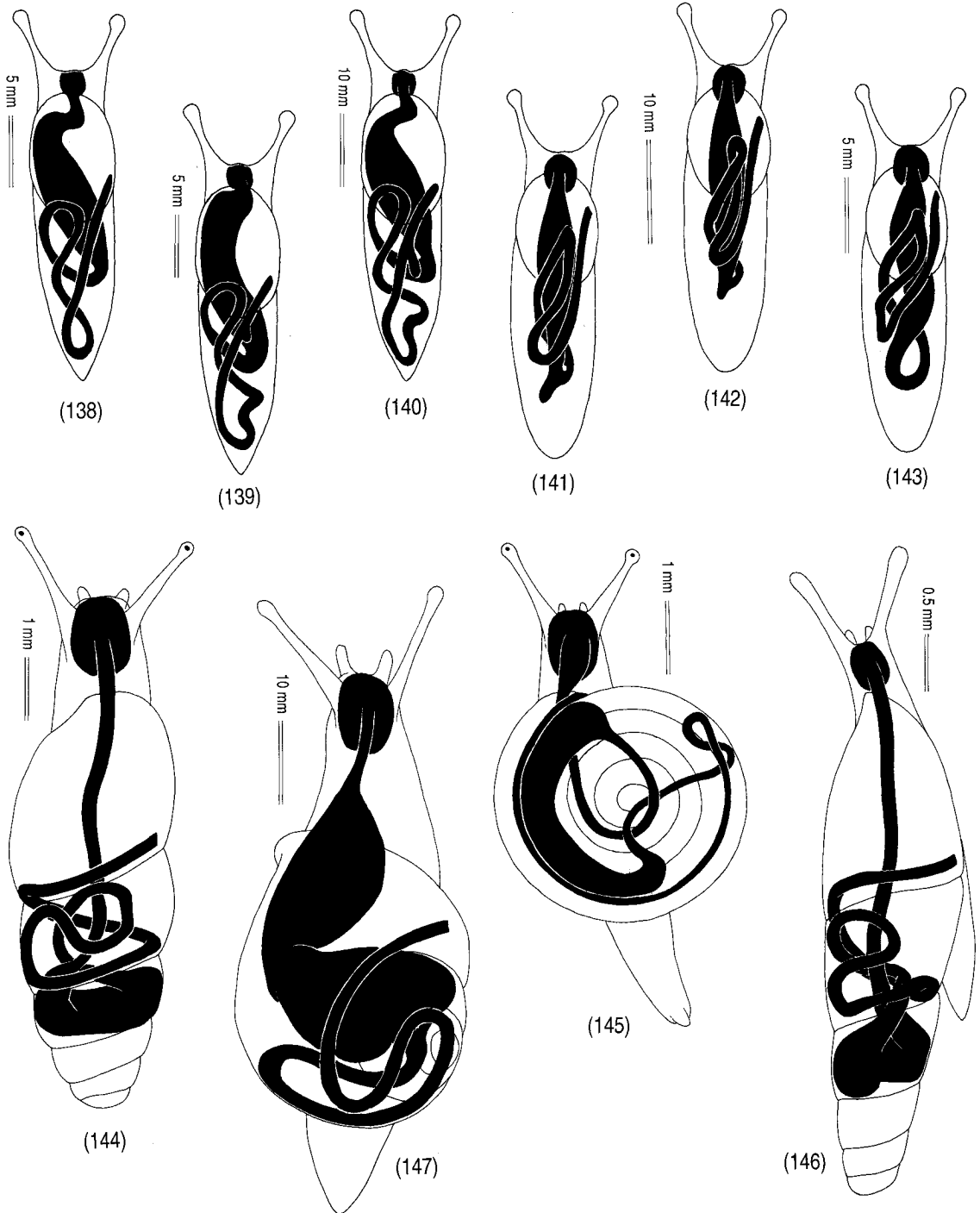
Fig. 138–147 Layout of digestive tract (schematic): (138) *Deroceras laeve*; (139) *D. panormitanum*; (140) *D. reticulatum*; (141) *Arion distinctus*; (142) *A. hortensis*; (143) *A. intermedius*; (144) *Cochlicopa lubrica*; (145) *Coneuplecta calculosa*; (146) *Cecilioides acicula*; (147) *Cantareus aspersus*.
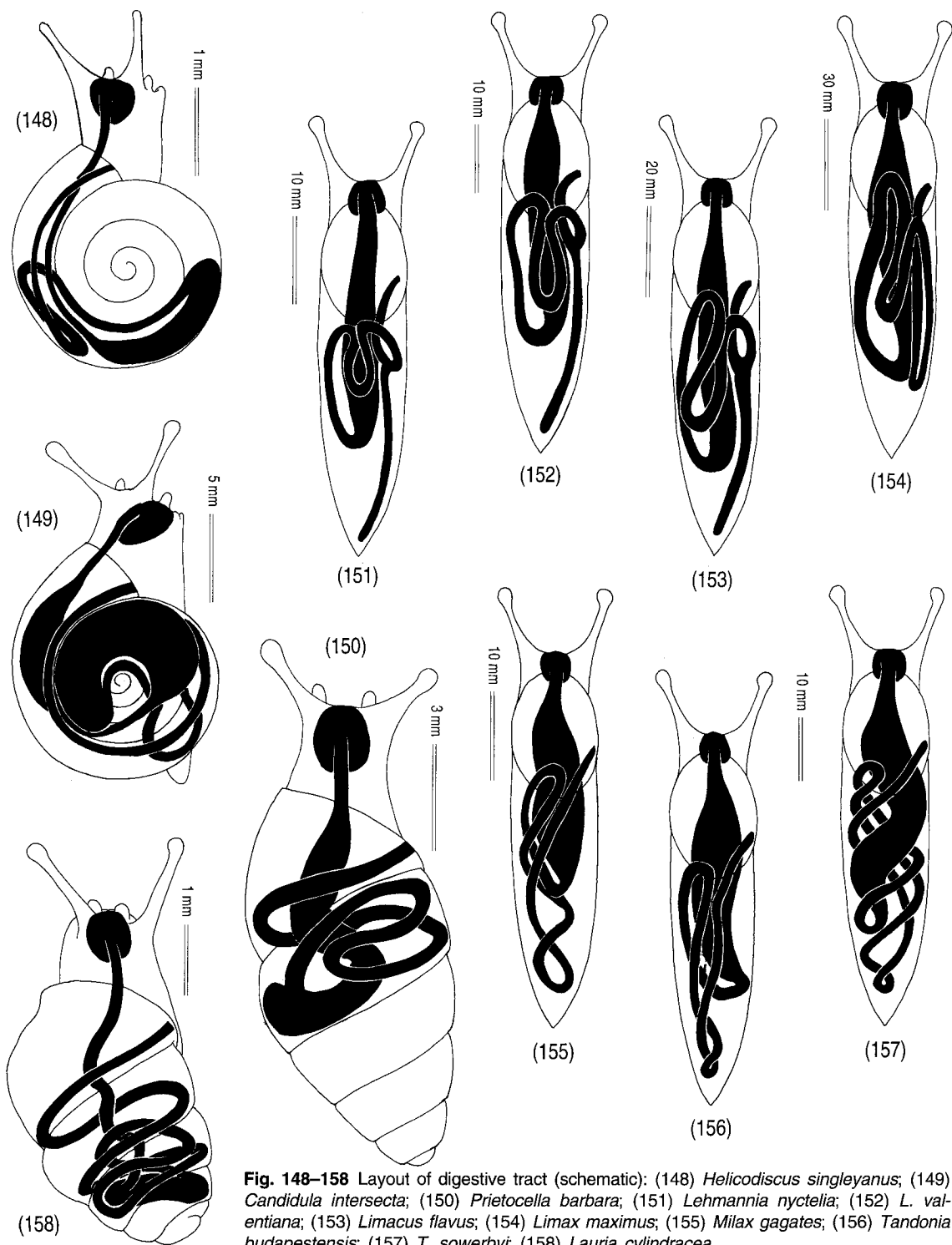
Fig. 148–158 Layout of digestive tract (schematic): (148) *Helicodiscus singleyanus*; (149) *Candidula intersecta*; (150) *Prietocella barbara*; (151) *Lehmannia nyctelia*; (152) *L. valentiana*; (153) *Limacus flavus*; (154) *Limax maximus*; (155) *Milax gagates*; (156) *Tandonia budapestensis*; (157) *T. sowerbyi*; (158) *Lauria cylindracea*.
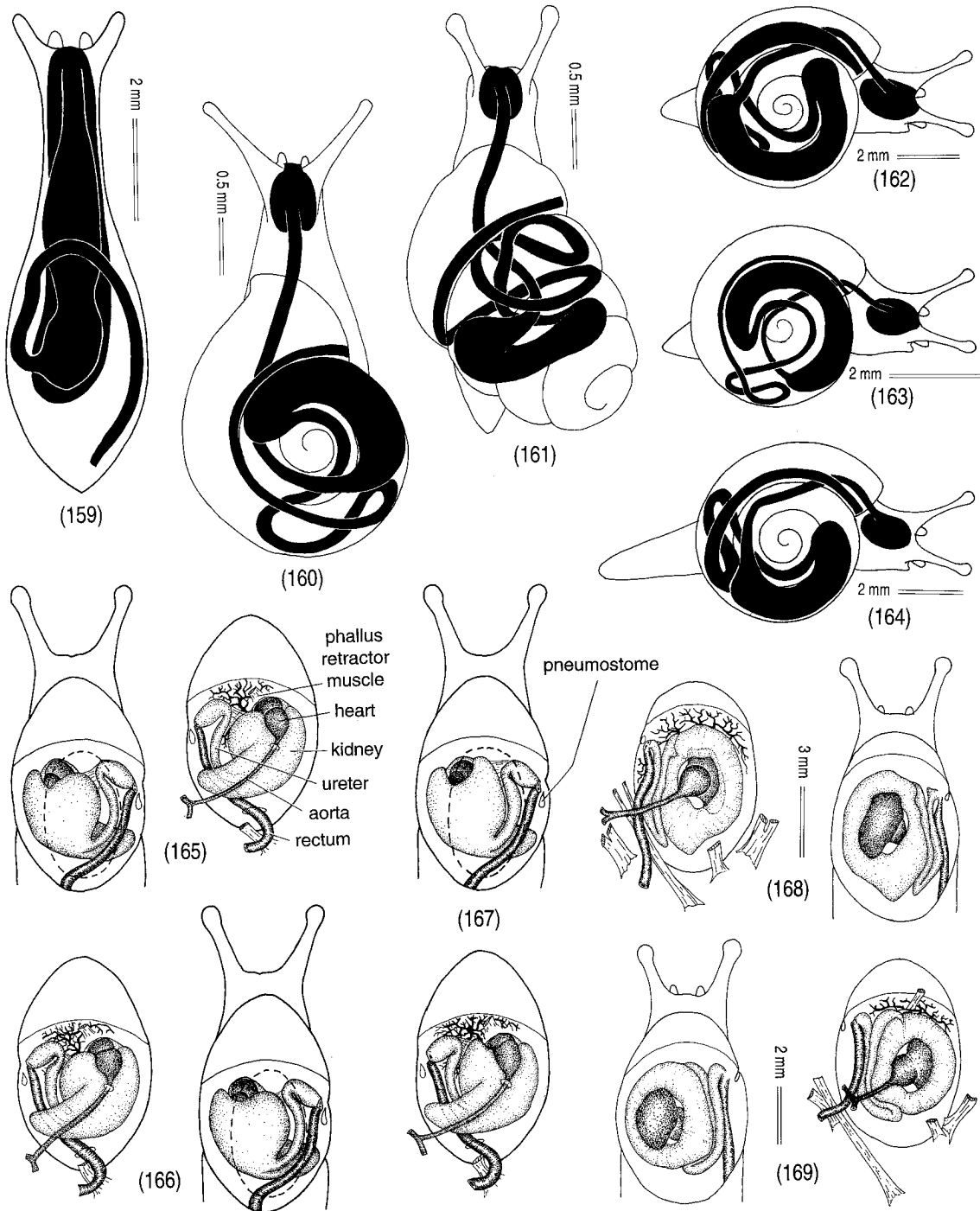
Fig. 159–164 Layout of digestive tract (schematic): (159) *Testacella haliotidea*; (160) *Vallonia excentrica*; (161) *Vertigo ovata*; (162) *Oxychilus alliarius*; (163) *Vitrea crystallina*; (164) *Zonitoides arboreus*. **Fig. 165–169** Layout of pallial organs: (165) *Deroceras laeve*, dorsal and ventral; (166) *D. panormitanum*, ventral and dorsal; (167) *D. reticulatum*, dorsal and ventral; (168) *Arion distinctus,* ventral and dorsal; (169) *A. intermedius*, dorsal and ventral.
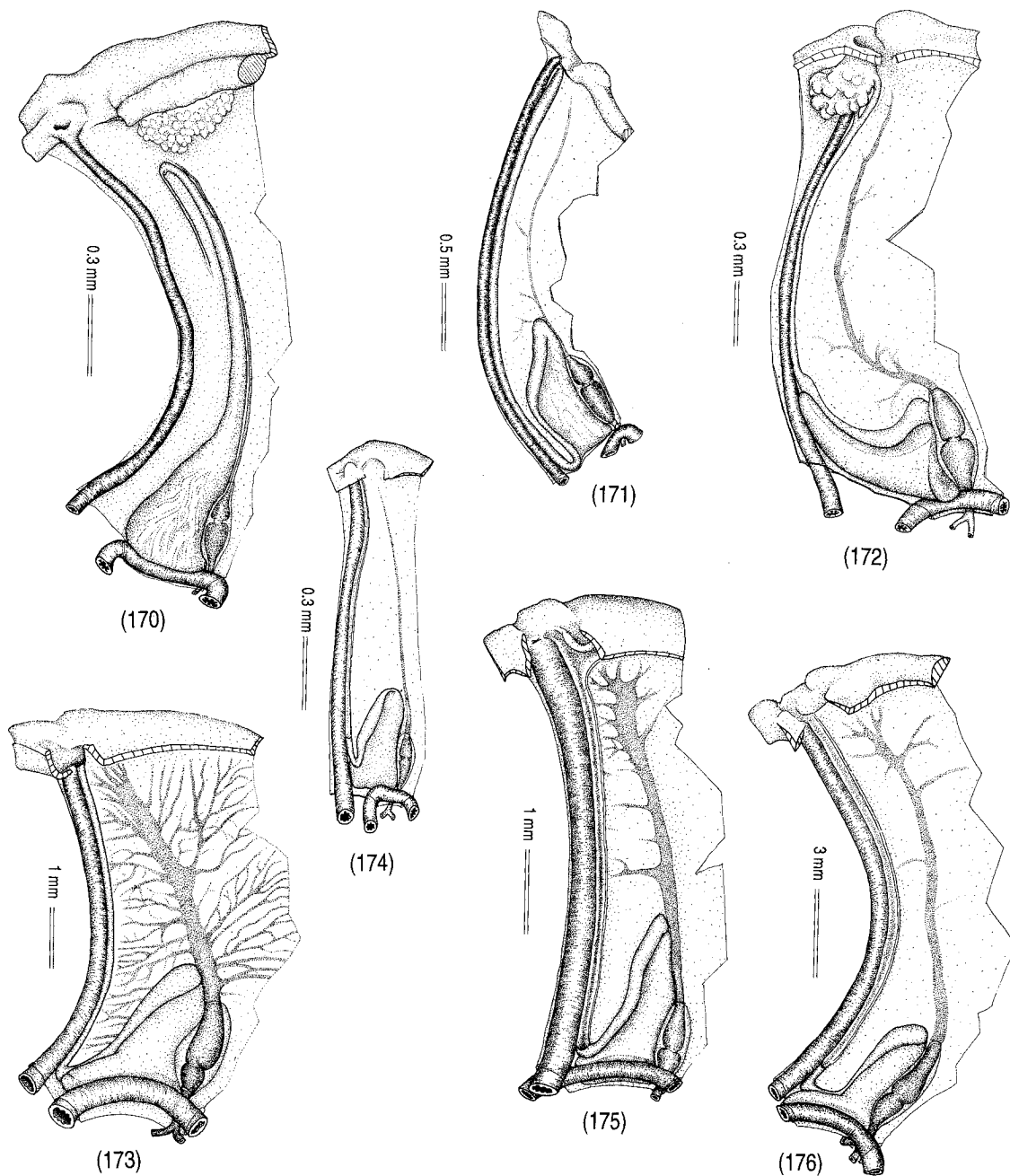
Fig. 170–176 Pallial organs, ventral: (170) *Cochlicopa lubrica*; (171) *Coneuplecta calculosa*; (172) *Cecilioides acicula*; (173) *Cantareus aspersus*; (174) *Helicodiscus singleyanus*; (175) *Candidula intersecta*; (176) *Prietocella barbara*.
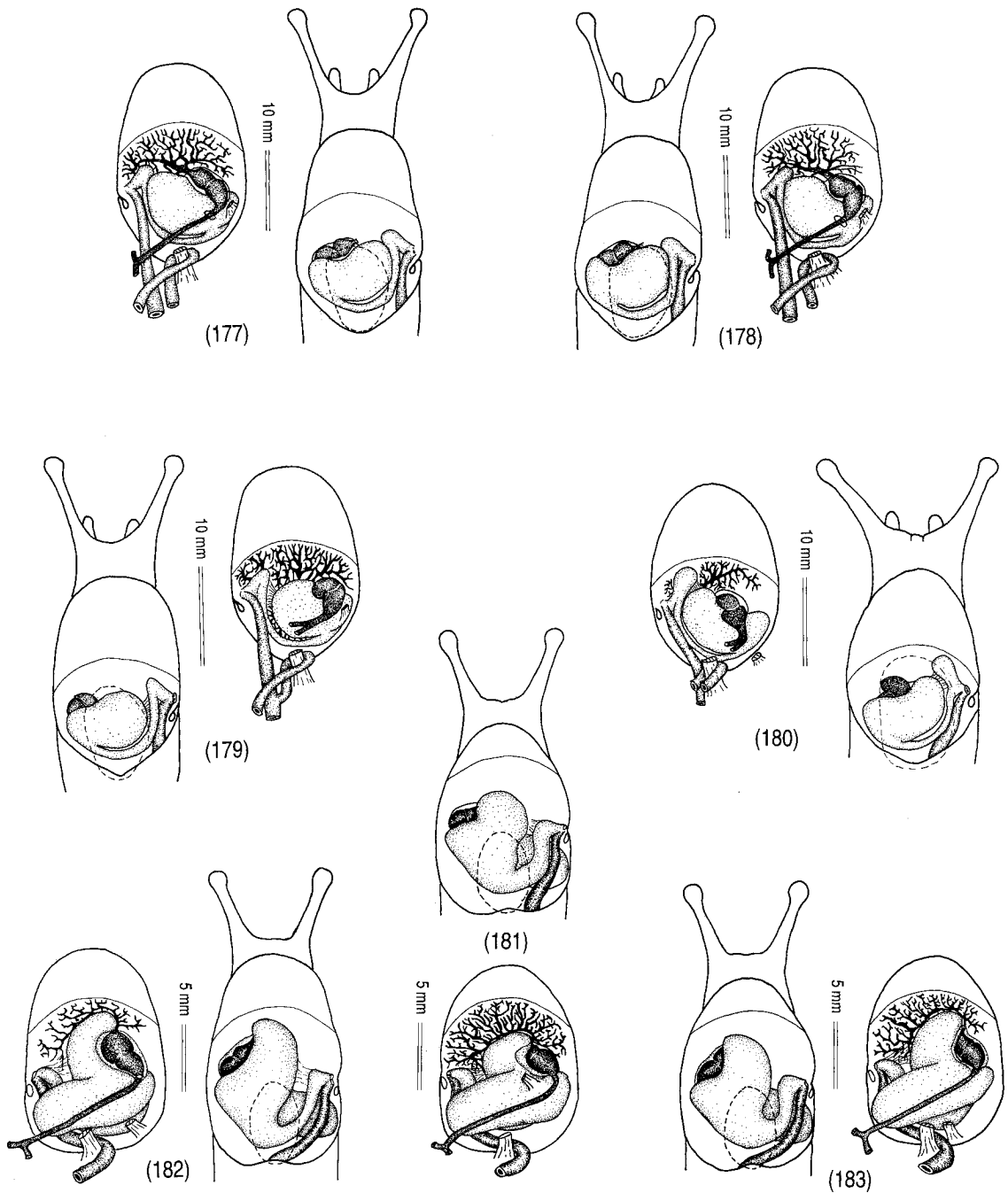
Fig. 177–183 Layout of pallial organs: (177) *Lehmannia nyctelia*, ventral and dorsal; (178) *L. valentiana*, dorsal and ventral; (179) *Limacus flavus*, dorsal and ventral; (180) *Limax maximus*, dorsal and ventral; (181) *Milax gagates*, dorsal and ventral; (182) *Tandonia budapestensis*, ventral and dorsal; (183) *T. sowerbyi*, dorsal and ventral.
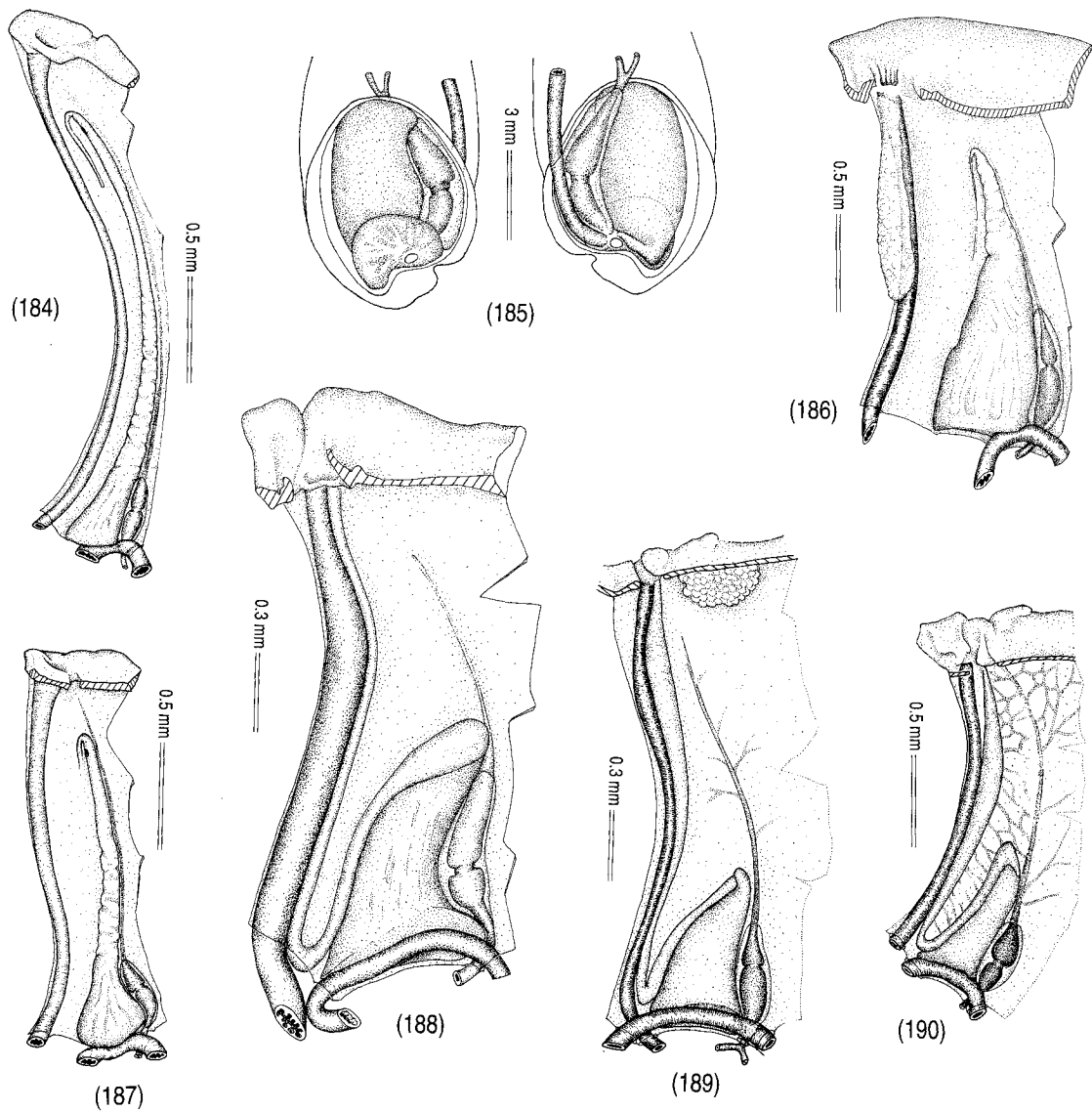
Fig. 184–190 Pallial organs: (184) *Lauria cylindracea*, ventral; (185) *Testacella haliotidea*, dorsal and ventral; (186) *Vallonia excentrica*, ventral; (187) *Vertigo ovata*, ventral; (188) *Oxychilus alliarius*, ventral; (189) *Vitrea crystallina*, ventral; (190) *Zonitoides arboreus*, ventral.

Fig. 191–199 Layout of free muscle system (schematic): (191) *Deroceras laeve*; (192a,b) *D. panormitanum*, with variation in derivation of buccal and right tentacular retractors; (193a–c) *D. reticulatum*, ditto; (194) *Arion distinctus*; (195) *A. intermedius*; (196) *Cochlicopa lubrica*; (197) *Coneuplecta calculosa*; (198) *Cecilioides acicula*; (199) *Cantareus aspersus*.
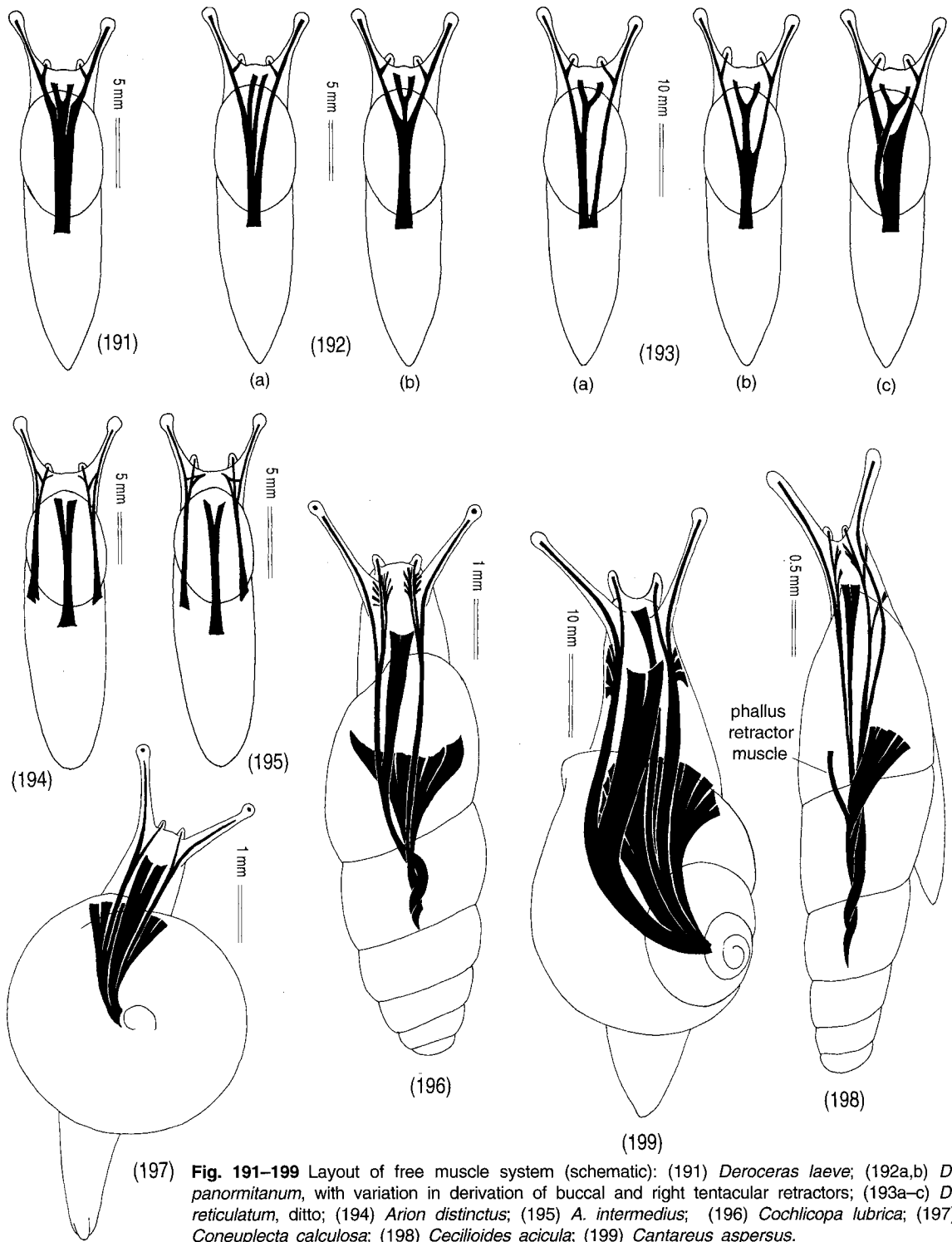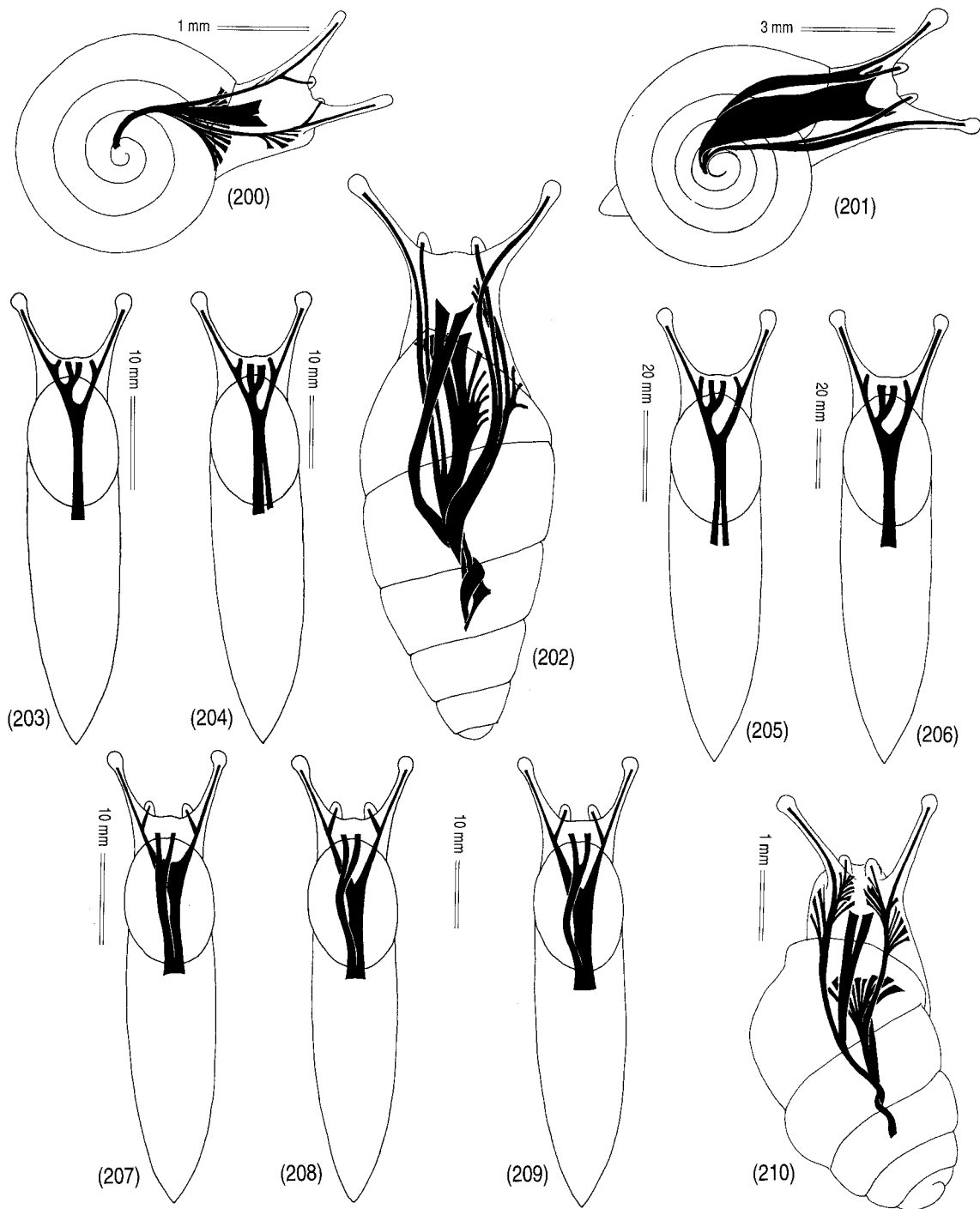
Fig. 200–210 Layout of free muscle system (schematic): (200) *Helicodiscus singleyanus*; (201) *Candidula intersecta*; (202) *Prietocella barbara*; (203) *Lehmannia nyctelia*; (204) *L. valentiana*; (205) *Limacus flavus*; (206) *Limax maximus*; (207) *Milax gagates*; (208) *Tandonia budapestensis*; (209) *T. sowerbyi*; (210) *Lauria cylindracea*.
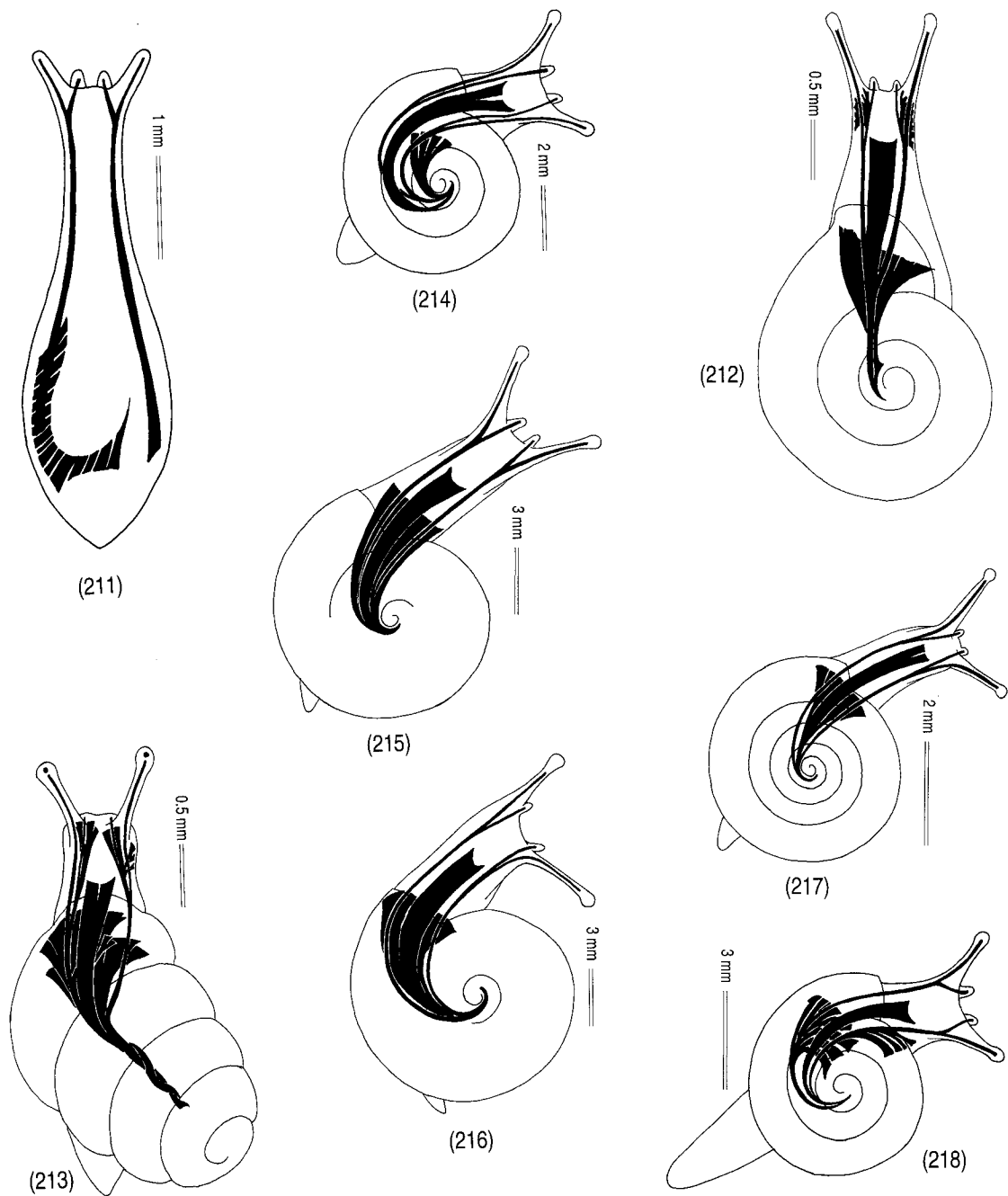
Fig. 211–218 Layout of free muscle system (schematic): (211) *Testacella haliotidea*; (212) *Vallonia excentrica*; (213) *Vertigo ovata*; (214) *Oxychilus alliarius*; (215) *O. cellarius*; (216) *O. draparnaudi*; (217) *Vitrea crystallina*; (218) *Zonitoides arboreus*.
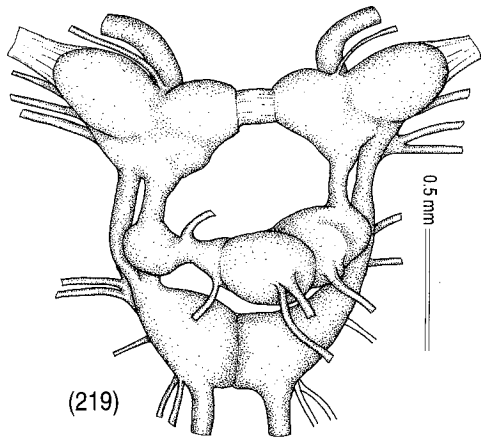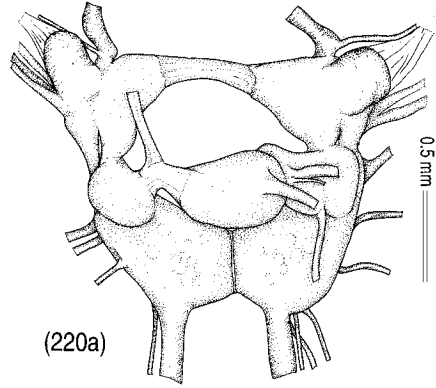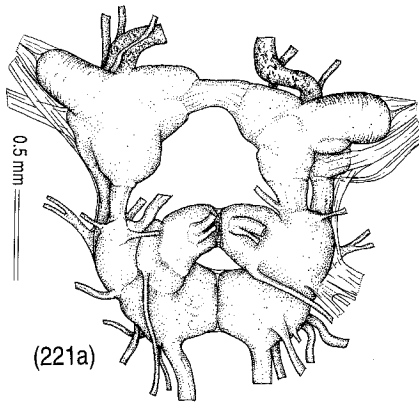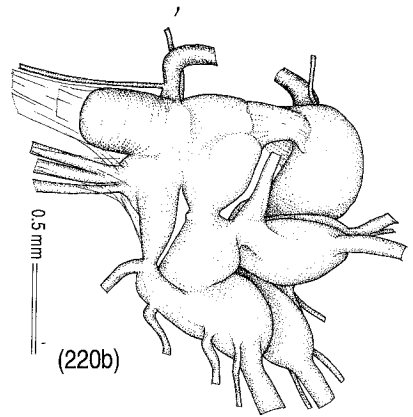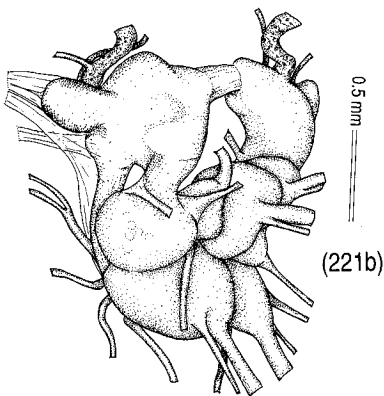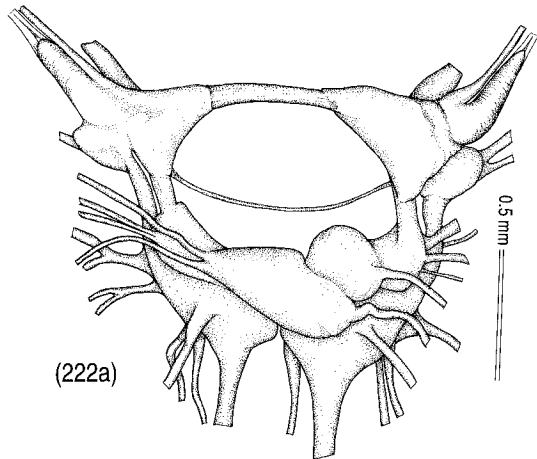
Fig. 219–222a Central nervous system: (219) *Deroceras laeve*, posterior; (220a,b) *D. panormitanum*, posterior and left posterolateral; (221a,b) *D. reticulatum*, posterior and left posterolateral; (222a) *Arion distinctus*, posterior.
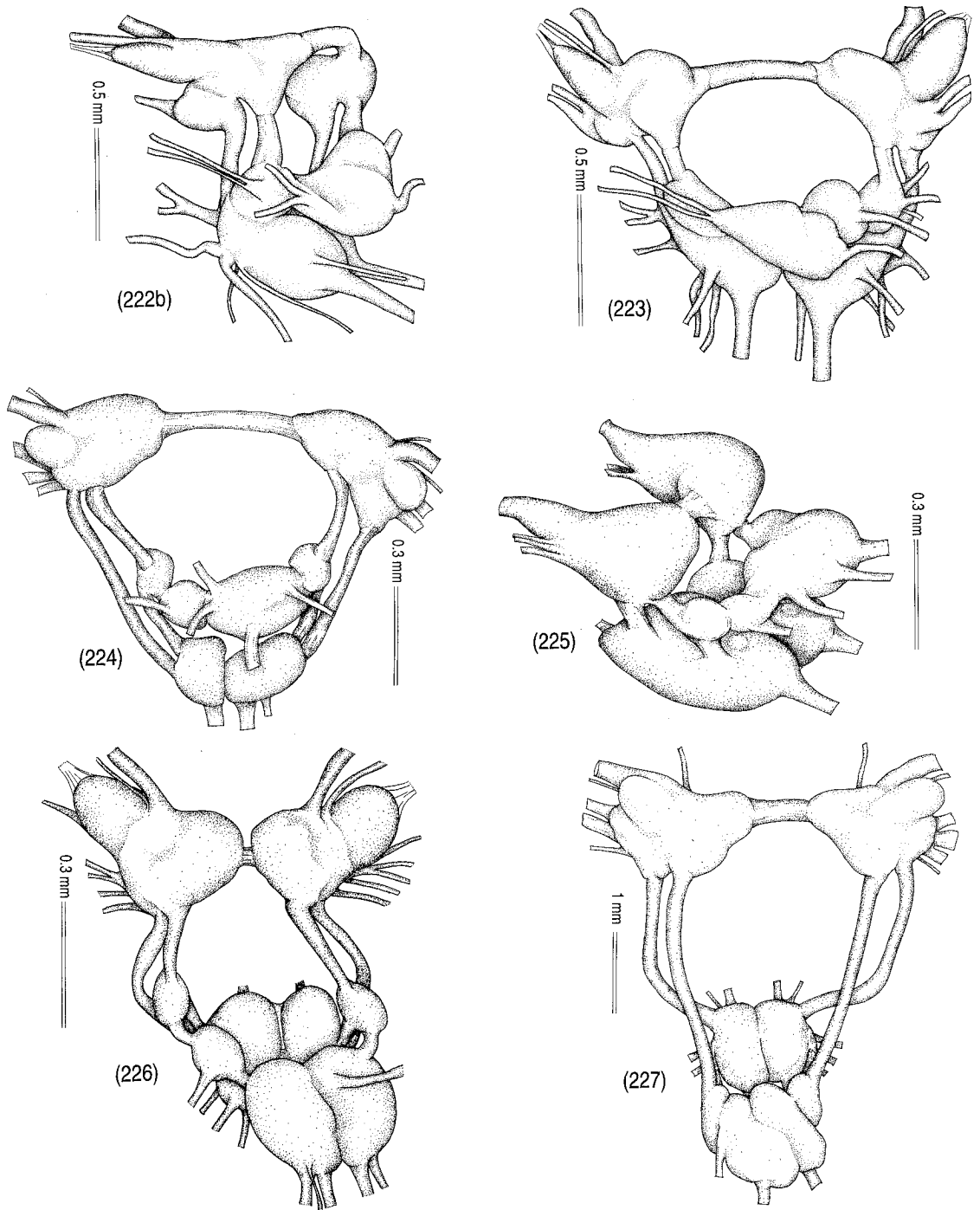
Fig. 222b–227 Central nervous system: (222b) *Arion distinctus*, left posterolateral; (223) *A. intermedius*, posterior; (224) *Cochlicopa lubrica*, posterior; (225) *Coneuplecta calculosa*, left posterolateral; (226) *Cecilioides acicula*, posterior; (227) *Cantareus aspersus*, posterior.
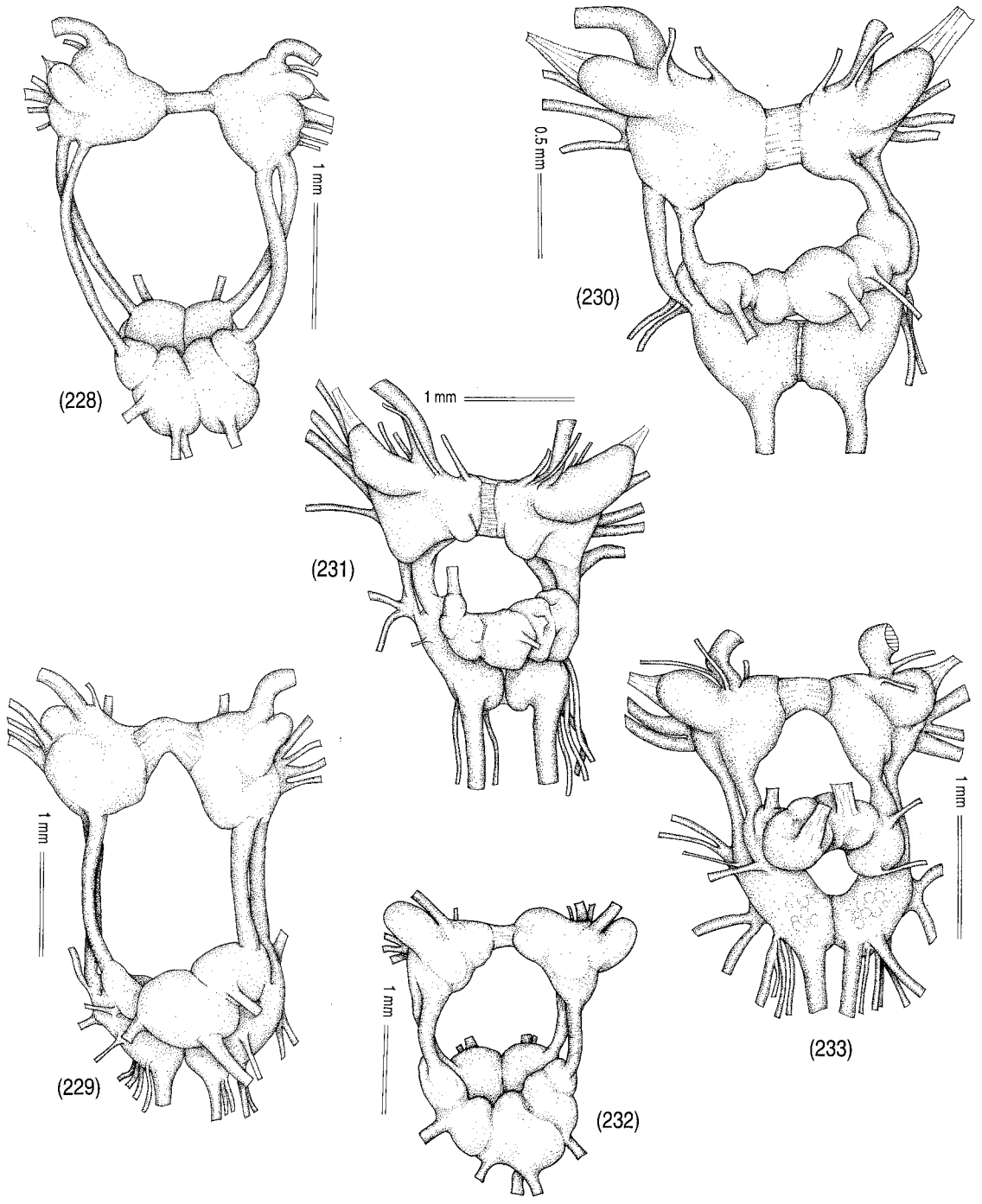
Fig. 228–233 Central nervous system: (228) *Candidula intersecta*; (229) *Prietocella barbara*; (230) *Lehmannia nyctelia*; (231) *L. valentiana*; (232) *Limax maximus*; (233) *Milax gagates*.
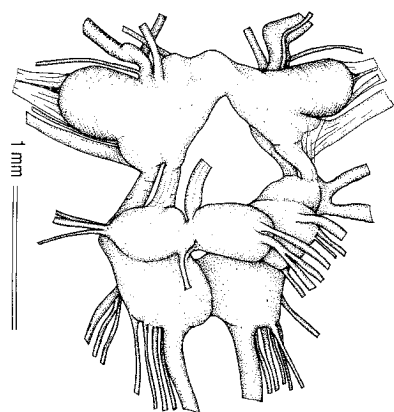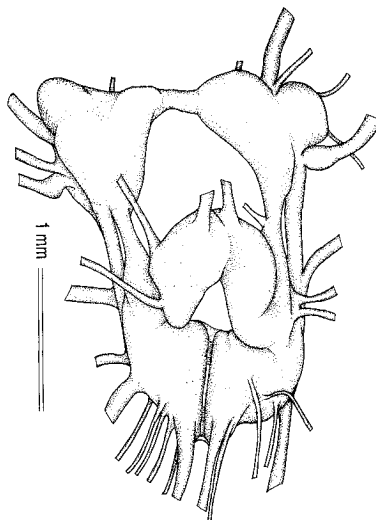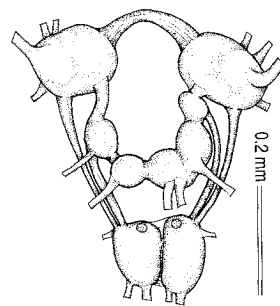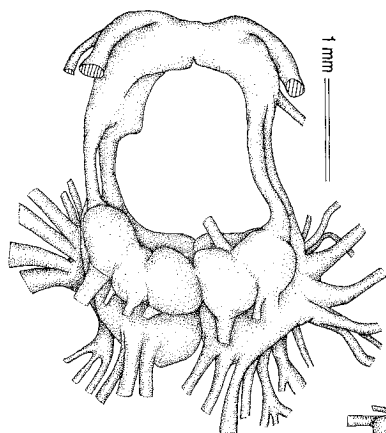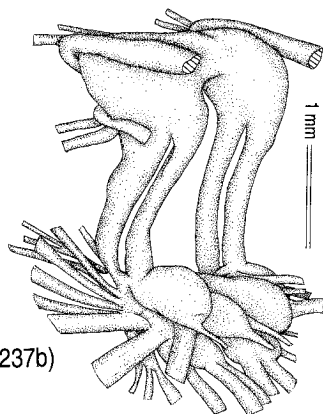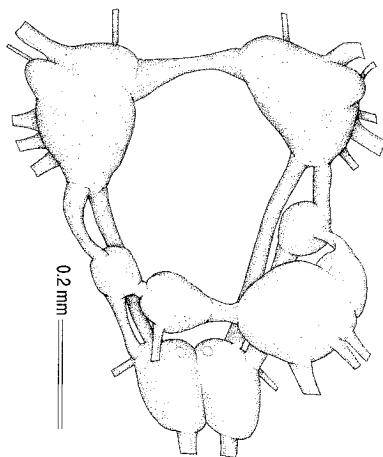
Fig. 234–238 Central nervous system: (234) *Tandonia budapestensis*, posterior; (235) *T. sowerbyi*, posterior; (236) *Lauria cylindracea*; posterior; (237a,b) *Testacella haliotidea*, posterior and left posterolateral; (238) *Vallonia excentrica*, posterior.
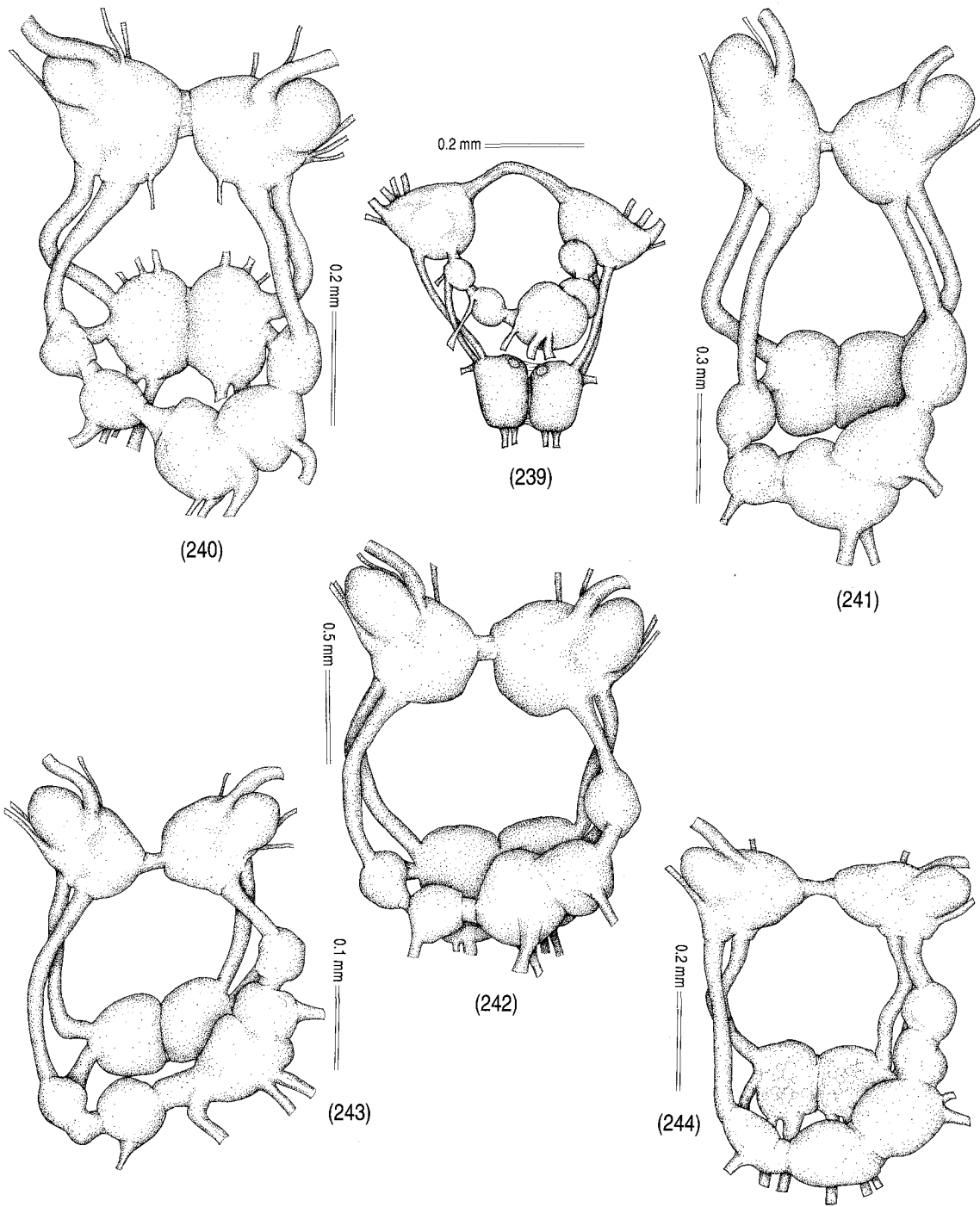
Fig. 239–244 Central nervous system, posterior: (239) *Vertigo ovata*; (240) *Oxychilus alliarius*; (241) *O. cellarius*; (242) *O. draparnaudi*; (243) *Vitrea crystallina*; (244) *Zonitoides arboreus.*

(245)
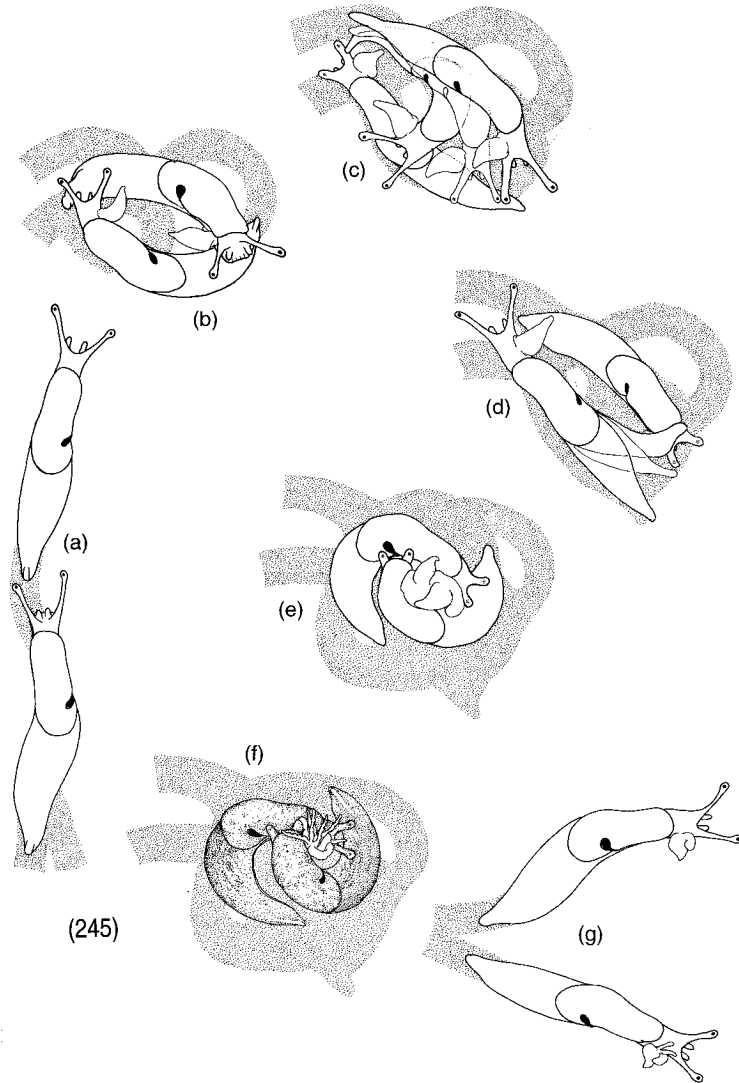
Fig. 245 Courtship and mating behaviour, *Deroceras panormitanum*.
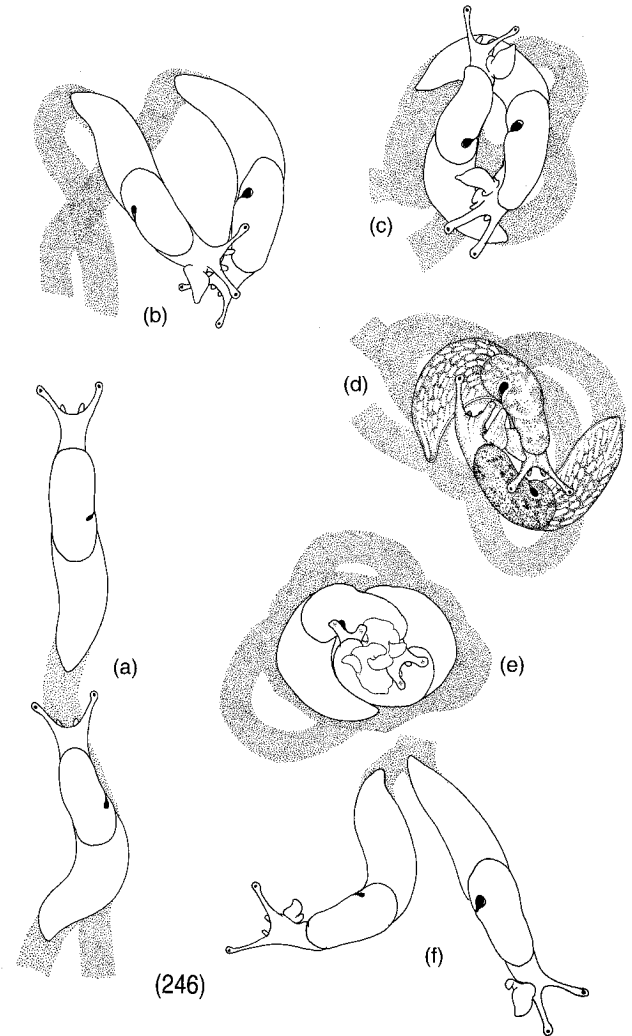
Fig. 246 Courtship and mating behaviour, *Deroceras reticulatum*.

(a)

(b)

(c)

(d)

(247)

(a)

(b)

(c)

(d)

(e)

(248)
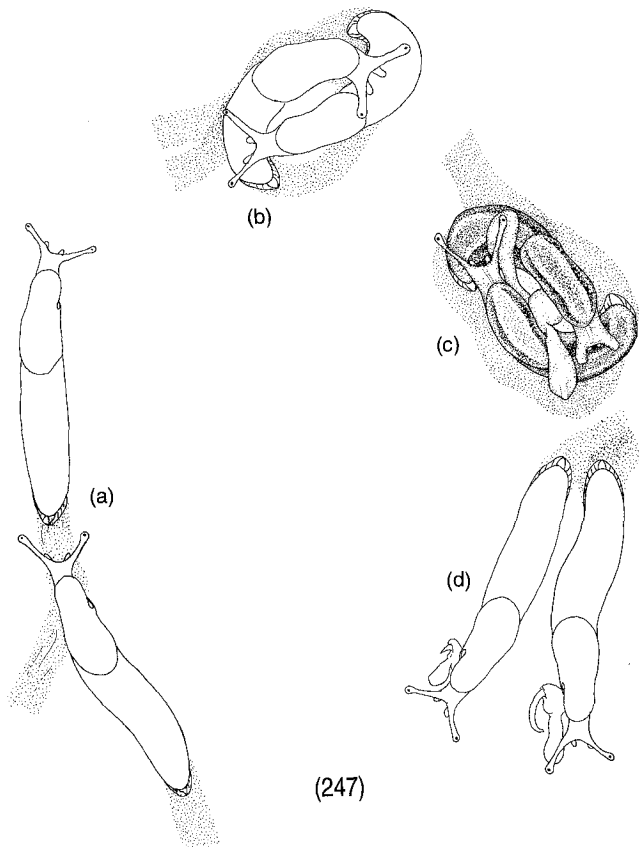
Fig. 247 Courtship and mating behaviour, *Arion hortensis*.
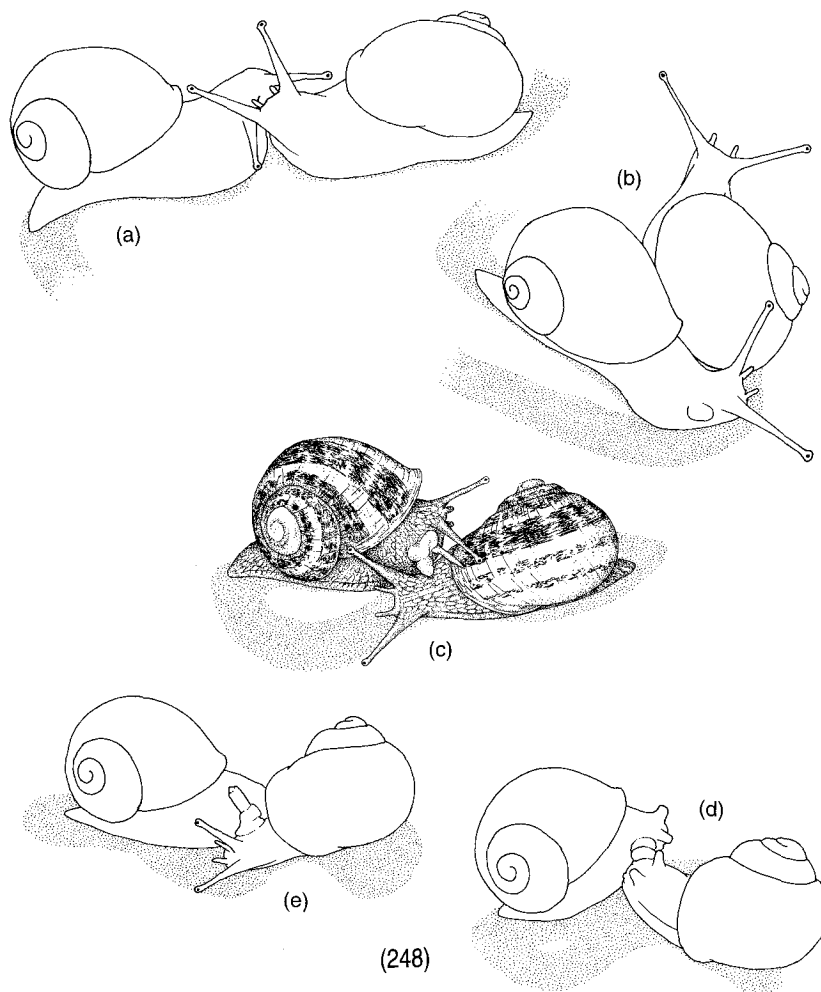
Fig. 248 Courtship and mating behaviour, *Cantareus aspersus*.
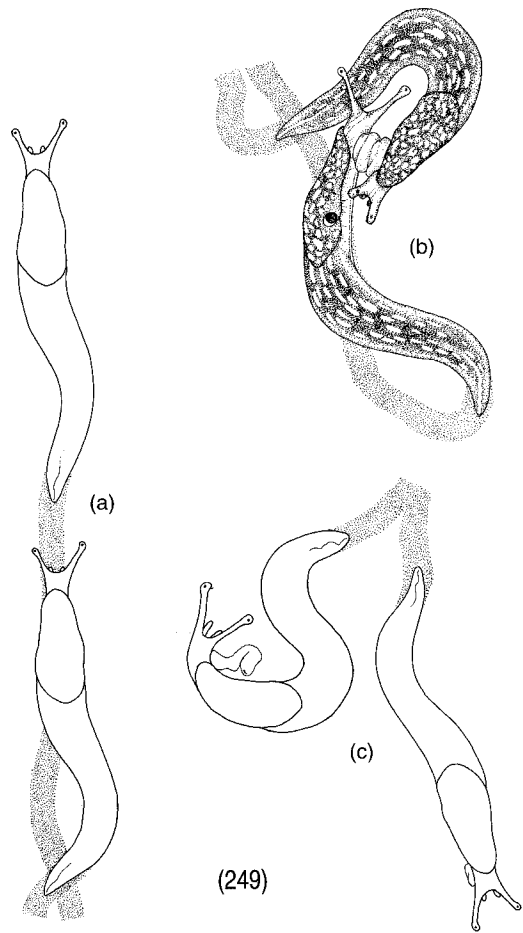
Fig. 249 Courtship and mating behaviour, *Limacus flavus*.
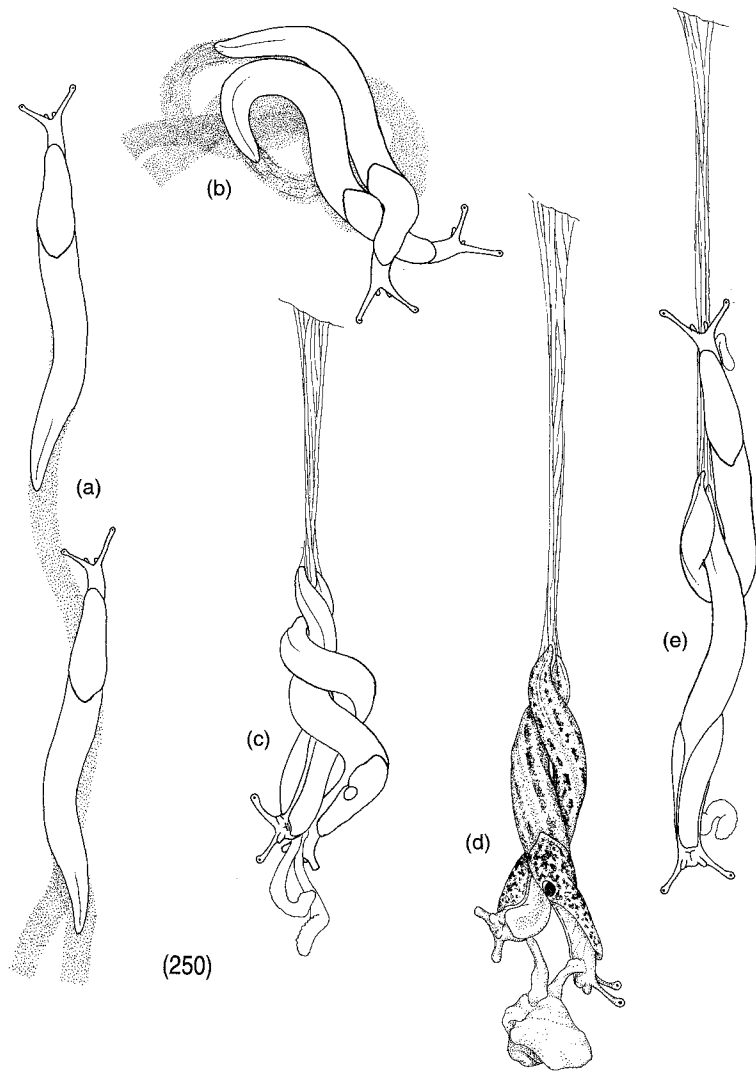
Fig. 250 Courtship and mating behaviour, *Limax maximus*.

(a)

(b)

(b)

(a)

(c)

(d)

(252)

(254)

(c)

(251)

(253)
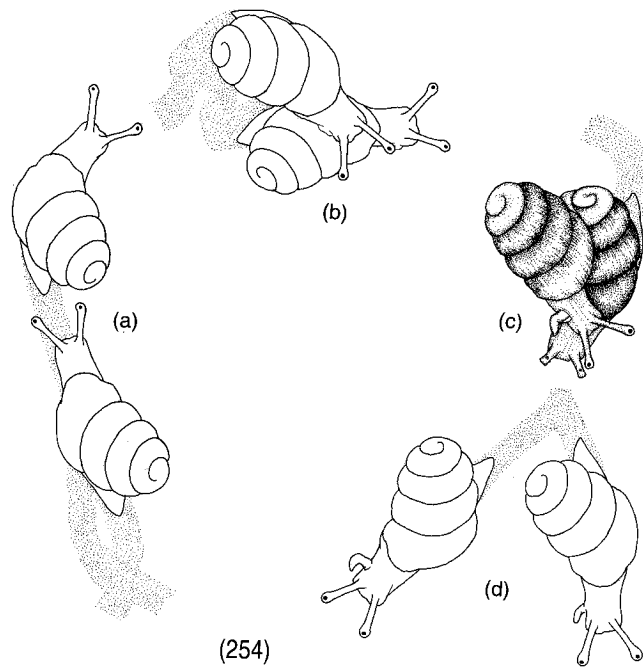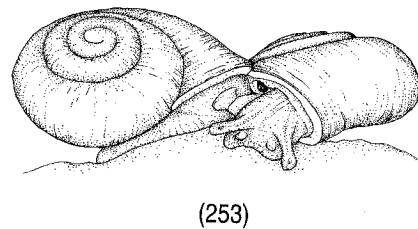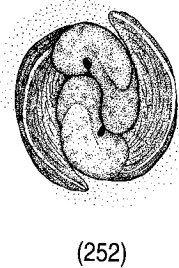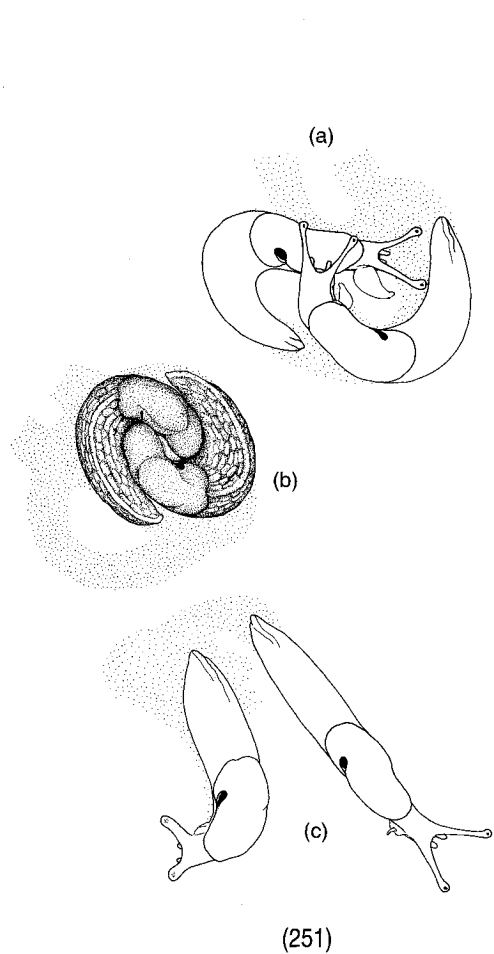
Fig. 251 Courtship and mating behaviour, *Milax gagates*.
Fig. 252, 253 Mating posture, *Tandonia budapestensis* and *Vallonia excentrica*.

Fig. 254 Courtship and mating behaviour, *Vertigo ovata*.
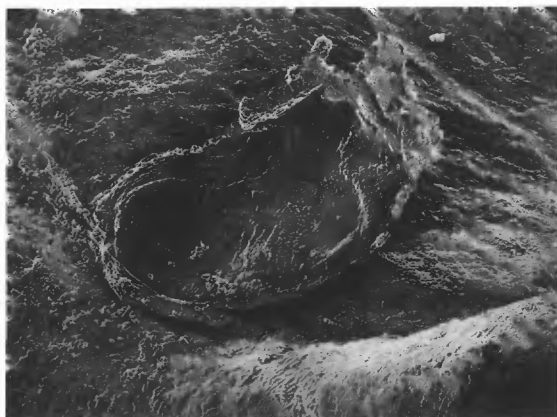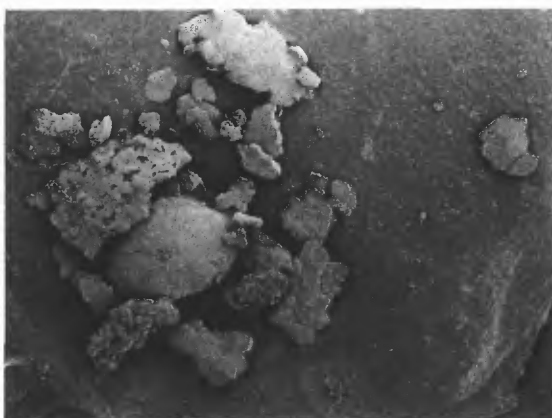
x65 [M1] [M2] x45
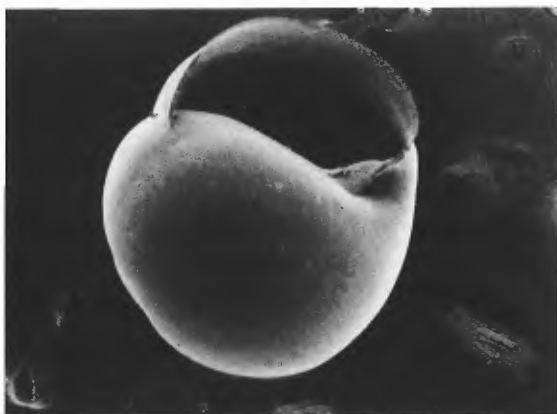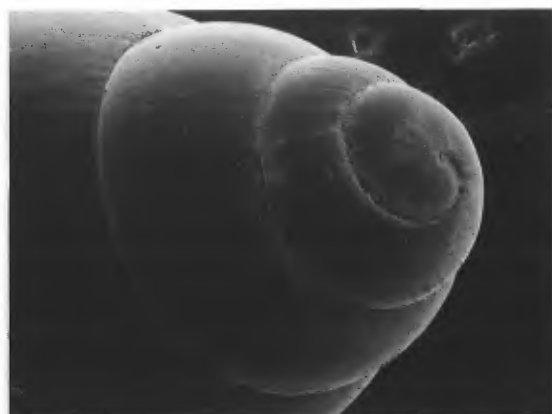
x75 [M3] [M4] x55
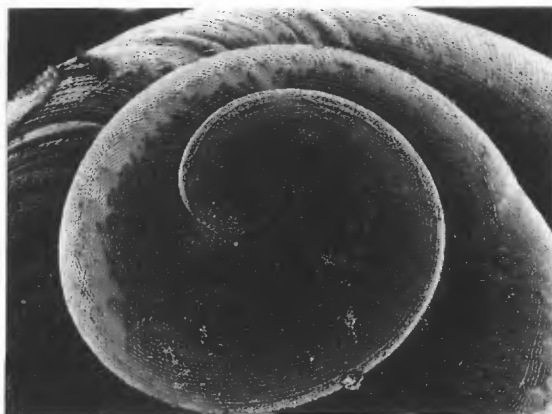
x120 [M5] [M6] x120

Fig. M1, 2 Shell granules, *Arion distinctus* and *A. intermedius*, ventral. **Fig. M3** Protoconch, *Cochlicopa lubrica* taken from egg, lateral. **Fig. M4** Shell apex, *C. lubrica*, dorsolateral. **Fig. M5, 6** Protoconch, *Coneuplecta calculosa*, shell apex, lateral and dorsolateral.
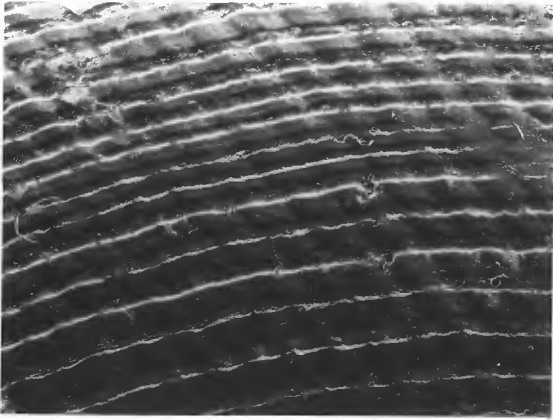
x990 [M7]
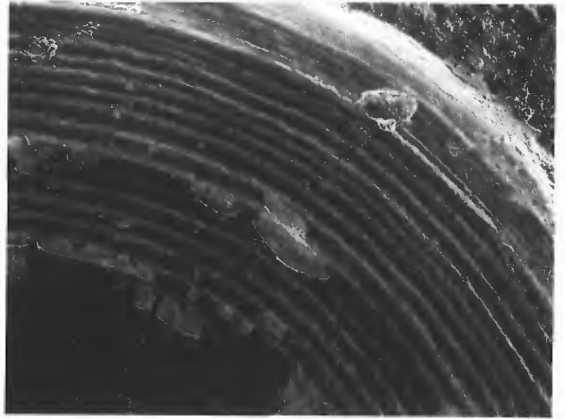
[M8] x660
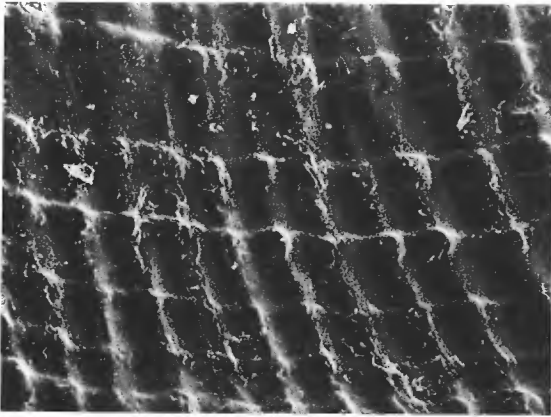
x1650 [M9]
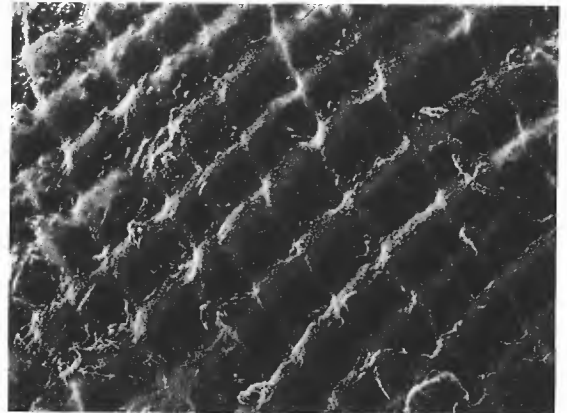
[M10] x1650
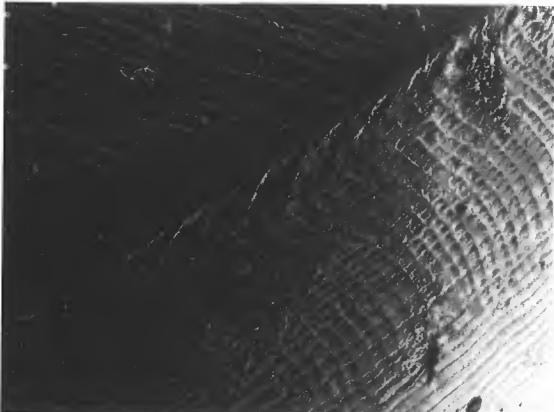
x330 [M11]
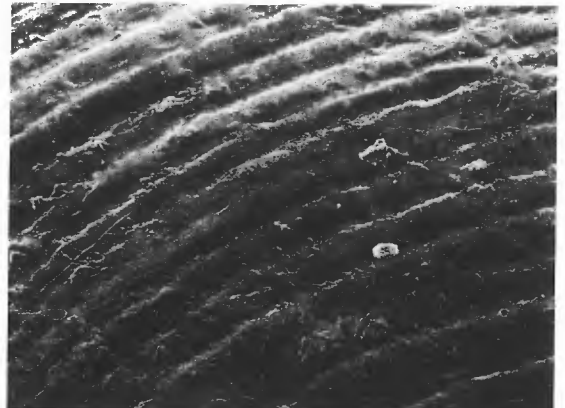
[M12] x1650

Fig. M7, 8 Protoconch, *Coneuplecta calculosa*, surface sculpture of early and late protoconch whorls. **Fig. M9–12** Teleoconch, *C. calculosa*: surface sculpture: (9, 10) dorsal surface; (11) at peripheral thread; (12) ventral surface.

–209–

x145 [M13]
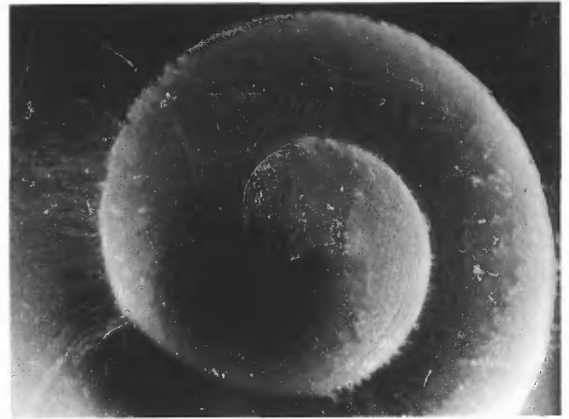
[M14] x110

x45 [M15]
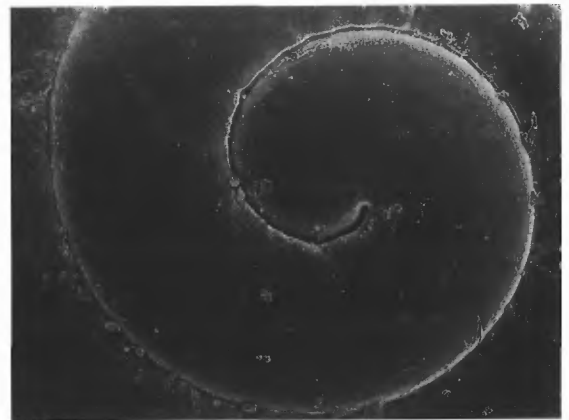
[M16] x220

x75 [M17]

[M18] x80

Fig. M13–18 Protoconch: (13, 14) *Cecilioides acicula*, lateral and dorsal; (15) *Cantareus aspersus*, dorsal; (16) *Helicodiscus singleyanus*, dorsal; (17) *Candidula intersecta*, dorsal; (18) *Prietocella barbara*, dorsolateral.

x100 [M19] [M20] x65

x110 [M21] [M22] x70
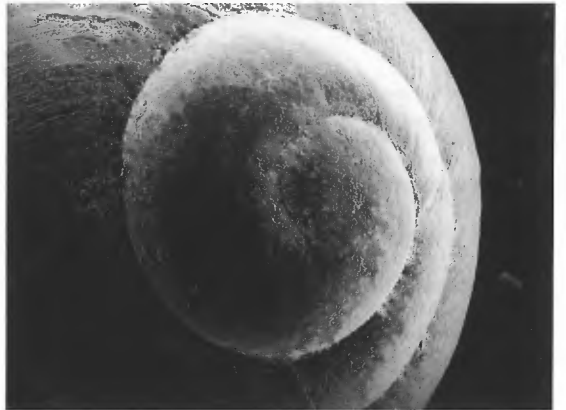
x145 [M23] [M24] x160

Fig. M19 Protoconch, *Lauria cylindracea*, dorsolateral. **Fig. M20** Shell aperture, *L. cylindracea*, showing parietal lamella. **Fig. M21, 22** Shells, *L. cylindracea* juveniles, showing columellar and parietal lamellae. **Fig. M23, 24** Protoconch: (23) *Vallonia excentrica*, dorsal; (24) *Vertigo ovata*, dorsolateral.

x110 [M25]   [M26] x95
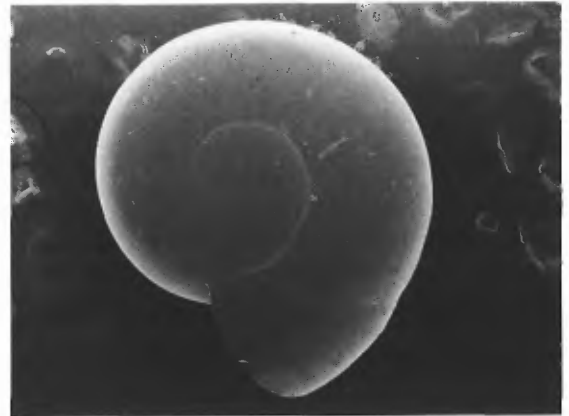
x55 [M27]   [M28] x45
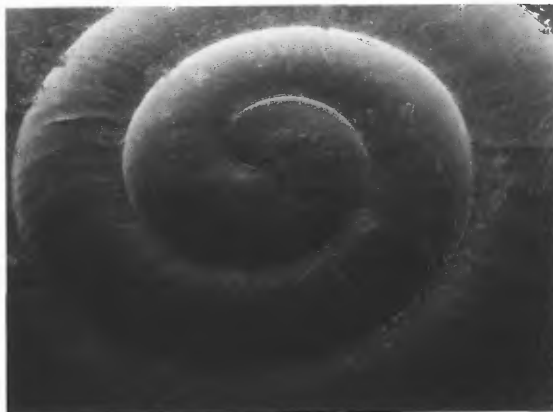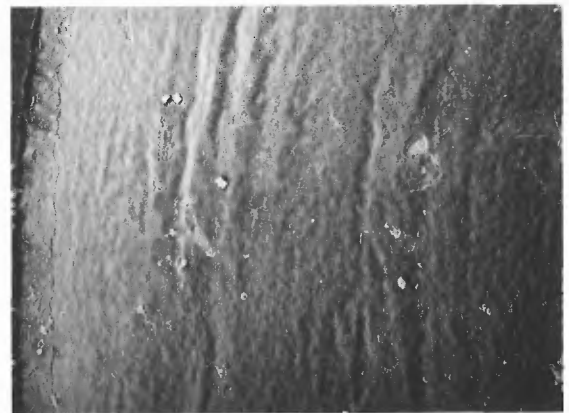
x120 [M29]   [M30] x1100

Fig. M25 Shell aperture, *Vertigo ovata*, showing barriers. **Fig. M26–30** Protoconch: (26) *Oxychilus alliarius*, dorsal; (27, 28) *O. cellarius* taken from egg, lateral and dorsal; (29, 30) *Vitrea crystallina*, dorsolateral, and surface sculpture.

x110   [M31]
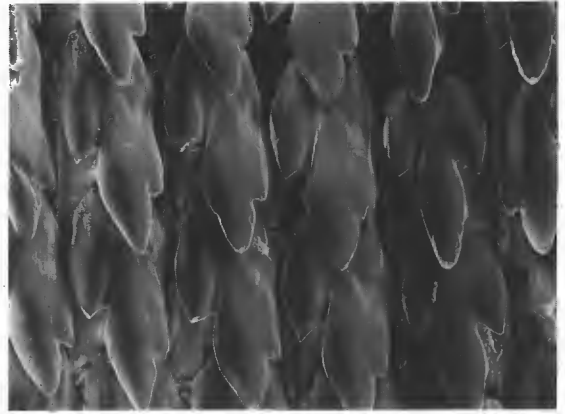
[M32]   x1100
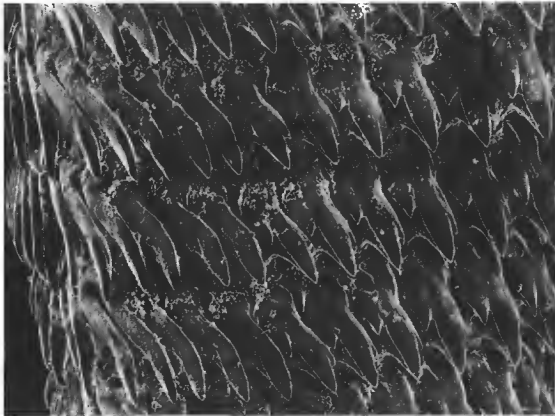
x1100   [M33]

[M34]   x1300
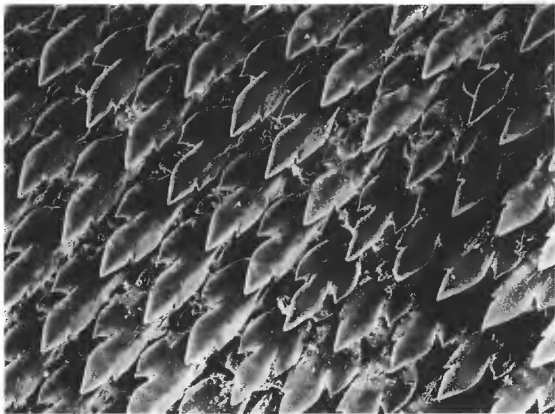
x880   [M35]
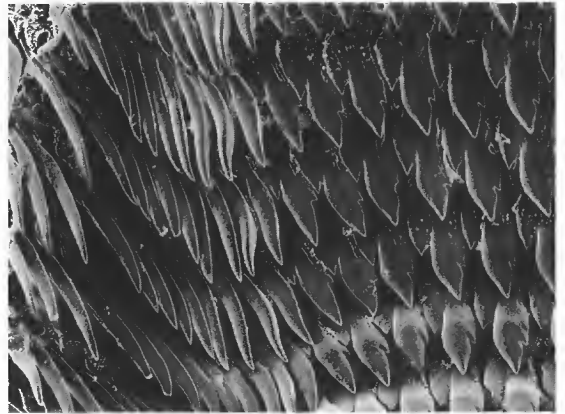
[M36]   x880

Fig. M31 Protoconch, *Zonitoides arboreus*, dorsolateral.
Fig. M32–36 Radular teeth: (32–34) *Deroceras laeve*; (35, 36) *D. panormitanum*.
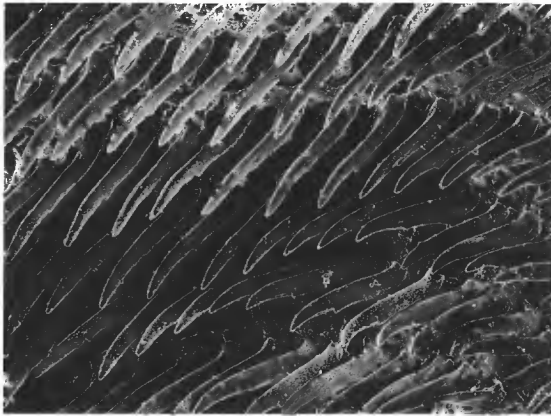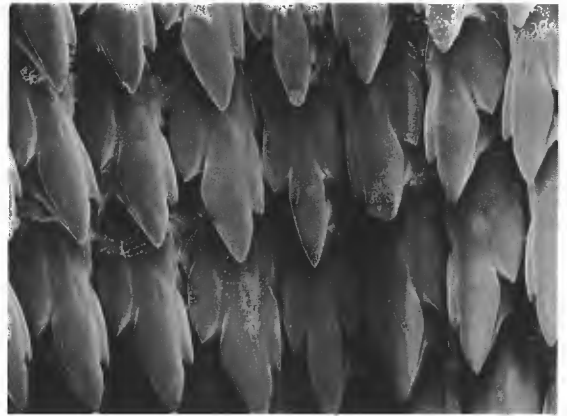
x1100   [M37]   [M38]   x720
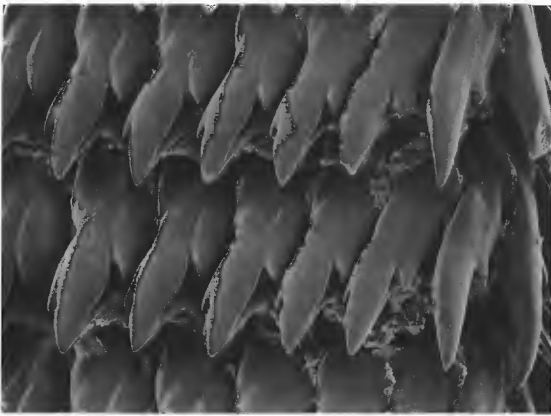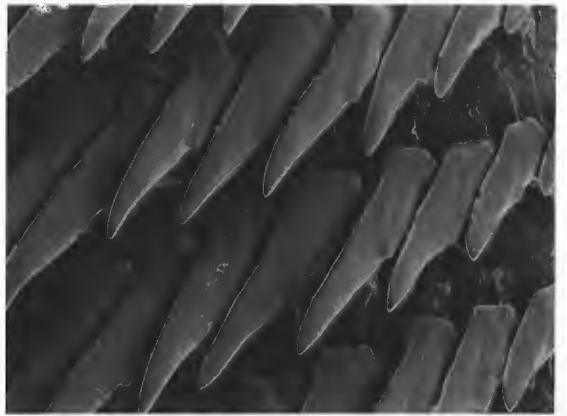
x800   [M39]   [M40]   x720
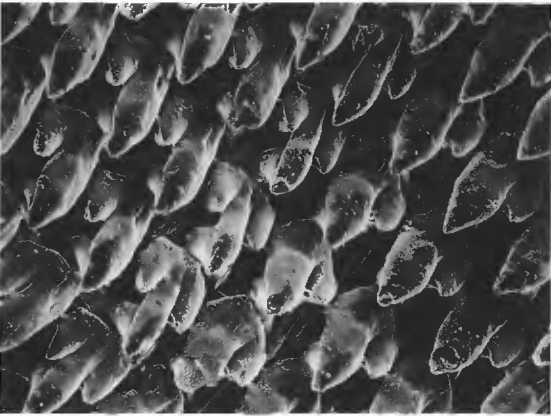
x1200   [M41]   [M42]   x500

Fig. M37–42 Radular teeth: (37) *Deroceras panormitanum*; (38–40) *D. reticulatum*; (41, 42) *Arion distinctus*.

x720 **[M43]**
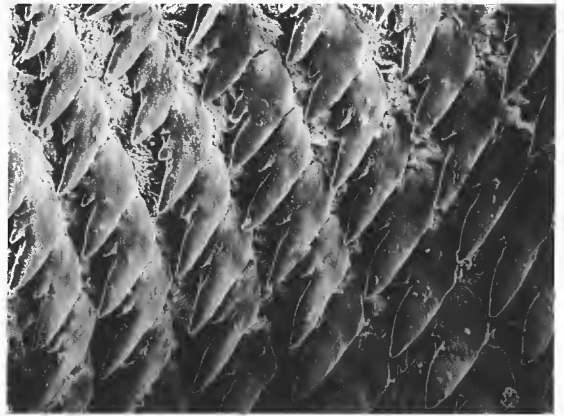
[M44] x1400
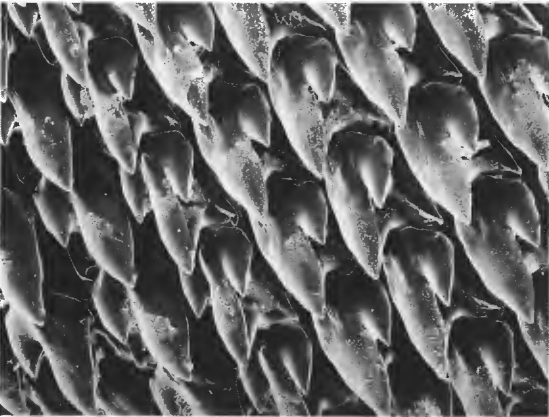
x1200 **[M45]**
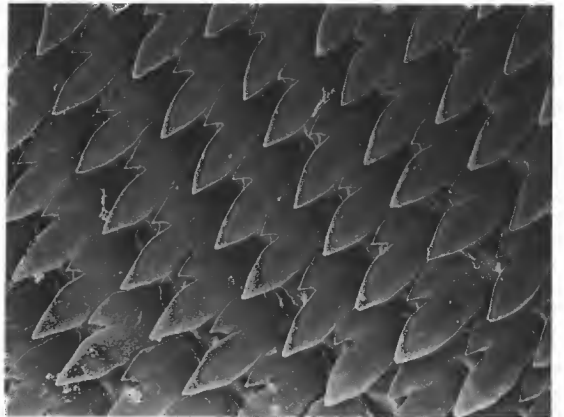
[M46] x1200
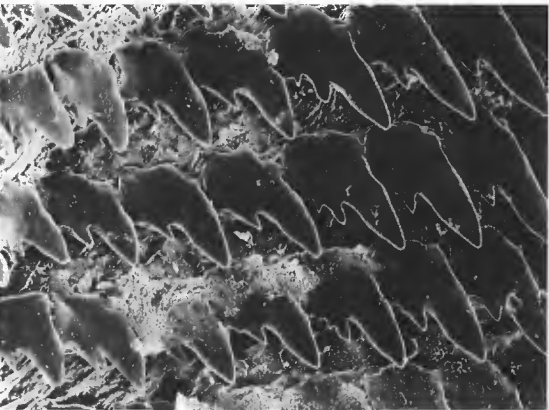
x1700 **[M47]**
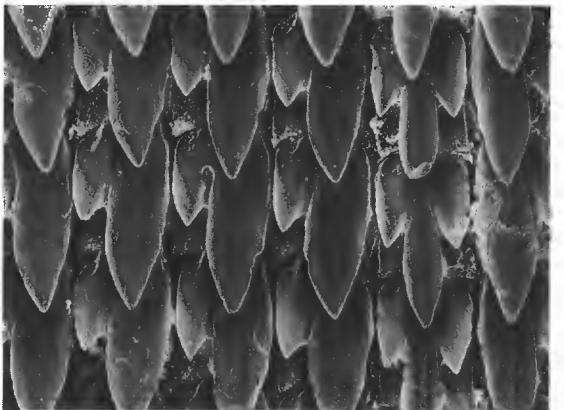
[M48] x720

Fig. M43–48 Radular teeth: (43, 44) *Arion distinctus*; (45–47) *A. hortensis*; (48) *A. intermedius*.
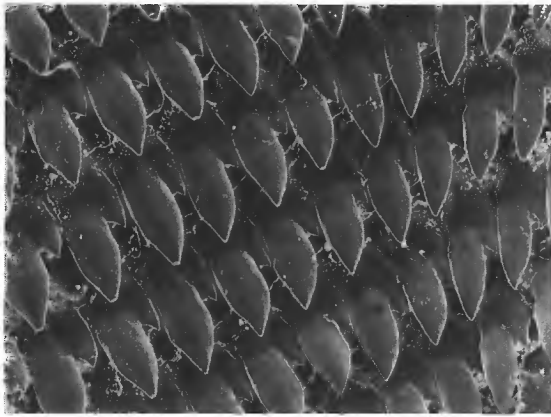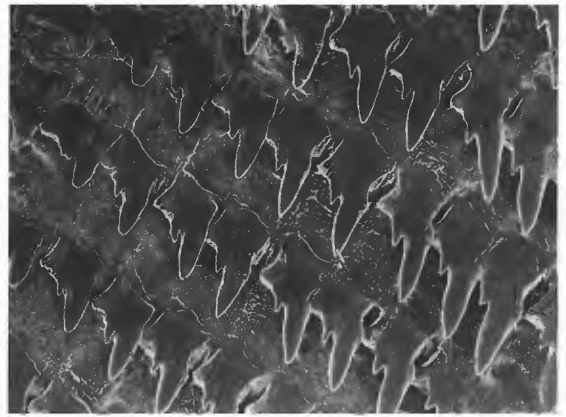
x720   [M49]   [M50]   x720
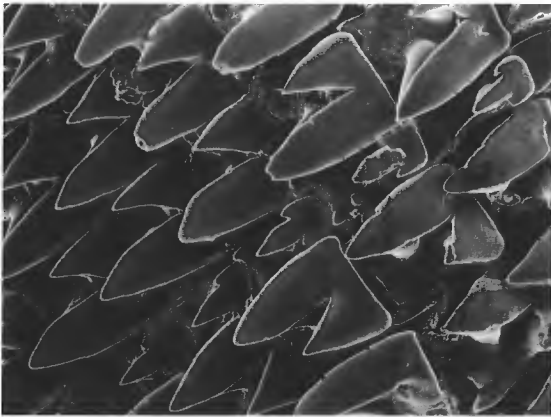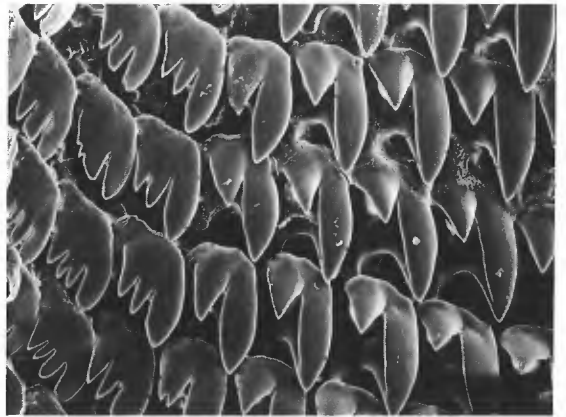
x2200   [M51]   [M52]   x2200
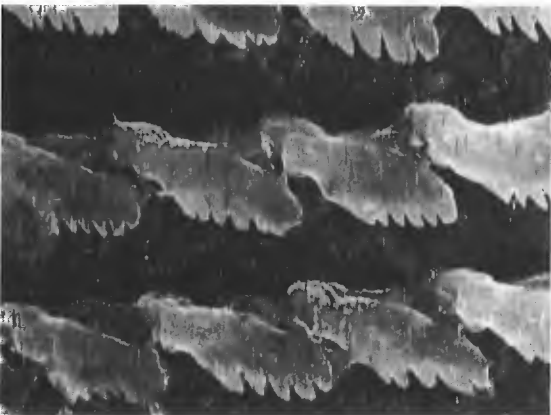
x2100   [M53]   [M54]   x5500

Fig. M49–54 Radular teeth: (49, 50) *Arion intermedius*; (51–53) *Cochlicopa lubrica*; (54) *Coneuplecta calculosa*.
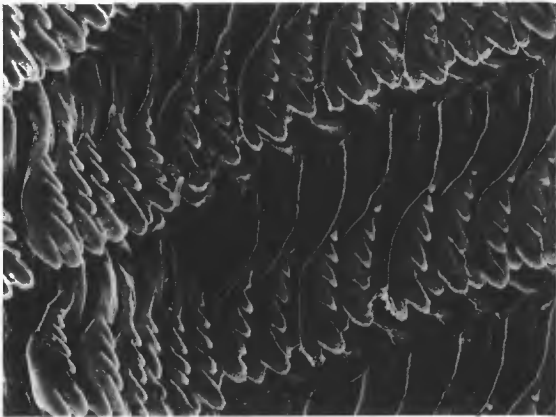
x3900 [M55]
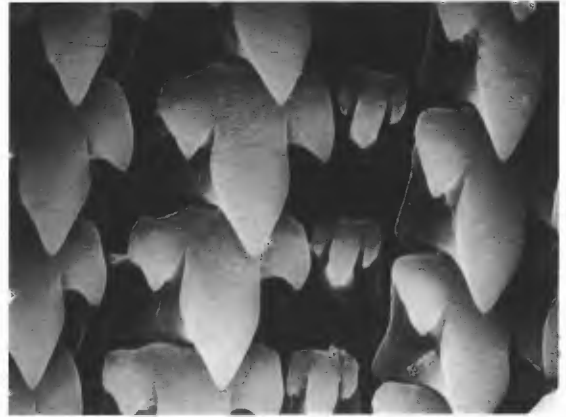
[M56] x4500
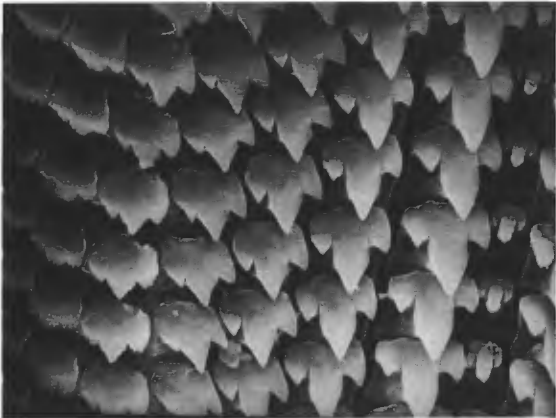
x2200 [M57]
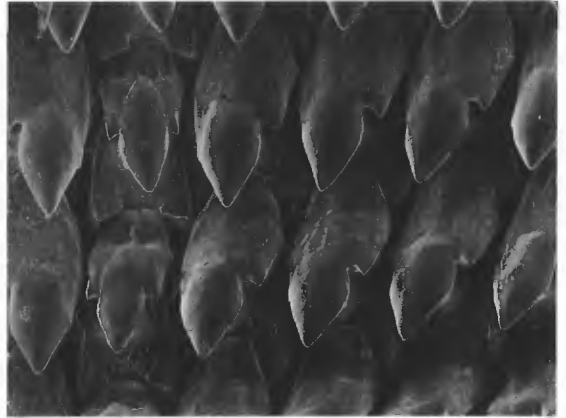
[M58] x550

x850 [M59]
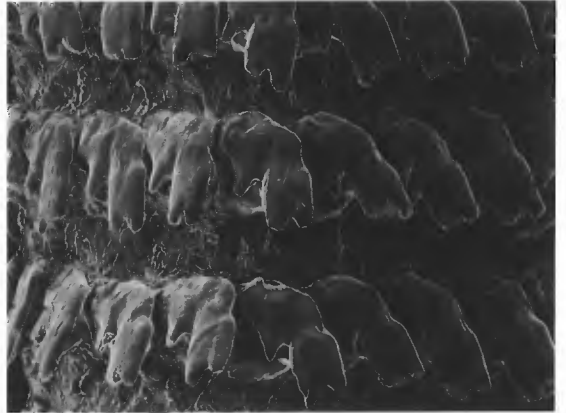
[M60] x550

Fig. M55–60 Radular teeth: (55) *Coneuplecta calculosa*; (56, 57) *Cecilioides acicula*; (58–60) *Cantareus aspersus*.
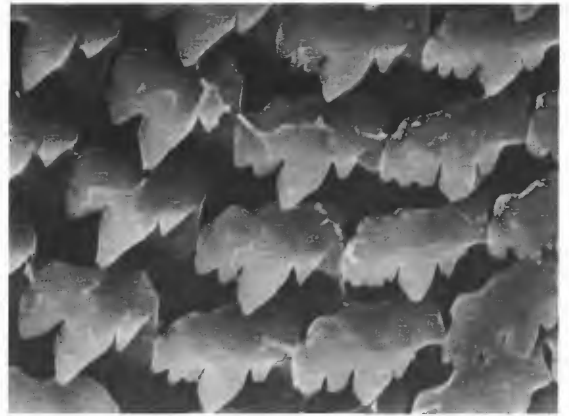
x4800   **[M61]**   **[M62]**   x4200
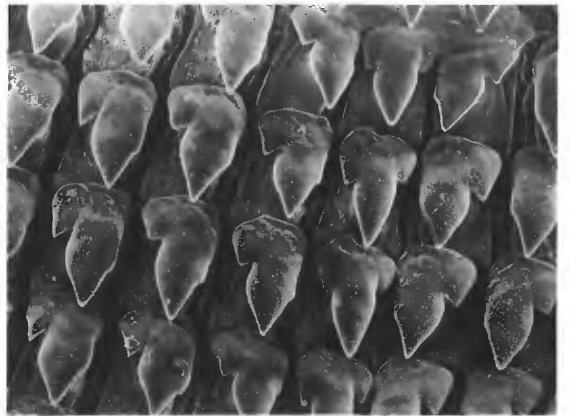
x6000   **[M63]**   **[M64]**   x1200
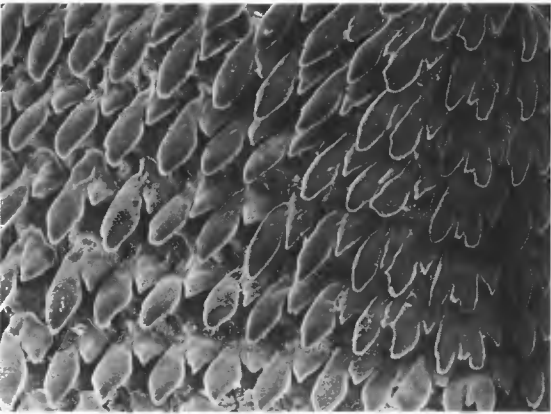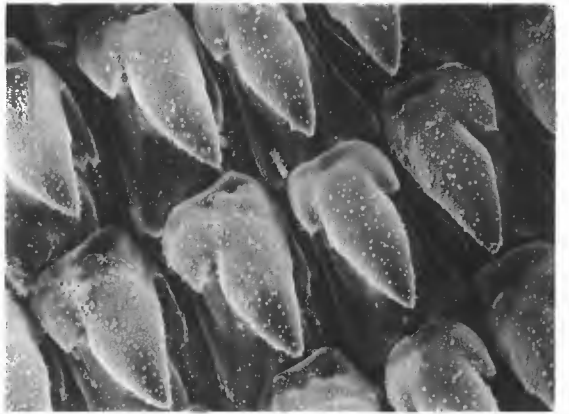
x1200   **[M65]**   **[M66]**   x2400

Fig. M61–66 Radular teeth: (61–63) *Helicodiscus singleyanus*; (64, 65) *Candidula intersecta*; (66) *Prietocella barbara*.
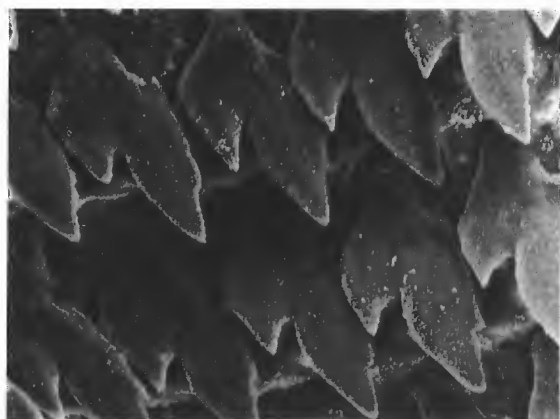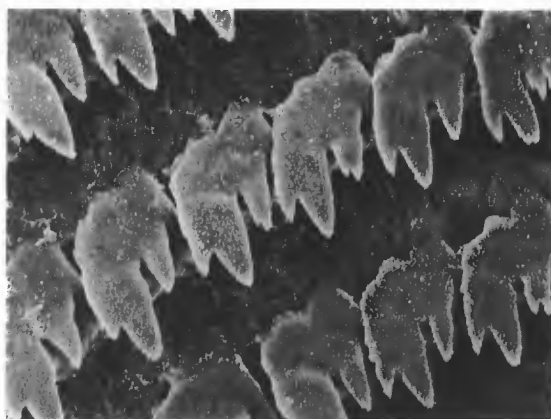
x2400 [M67] [M68] x2400
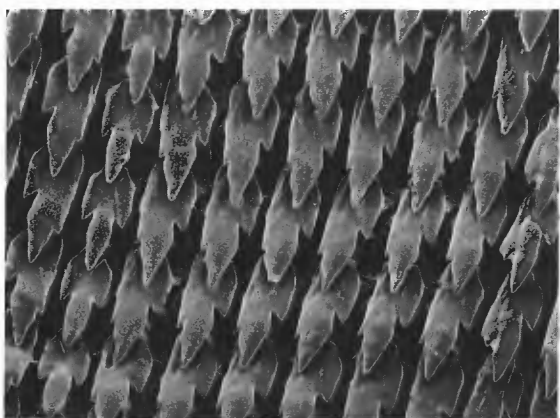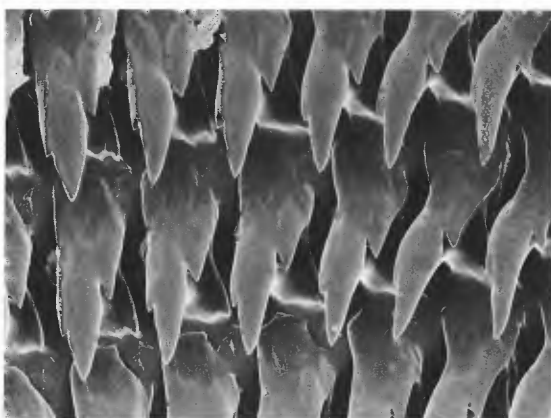
x880 [M69] [M70] x1300
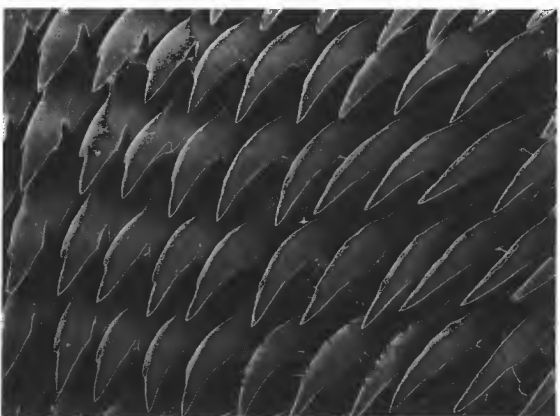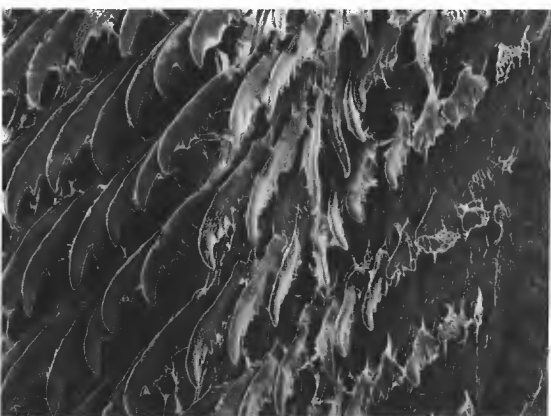
x990 [M71] [M72] x990

Fig. M67–72 Radular teeth: (67, 68) *Prietocella barbara*; (69–72) *Lehmannia nyctelia*.
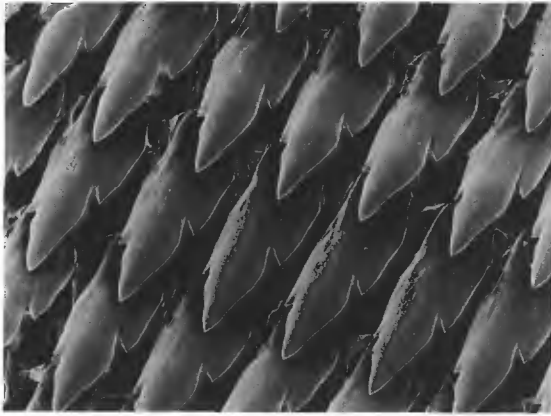
x650 [M73]
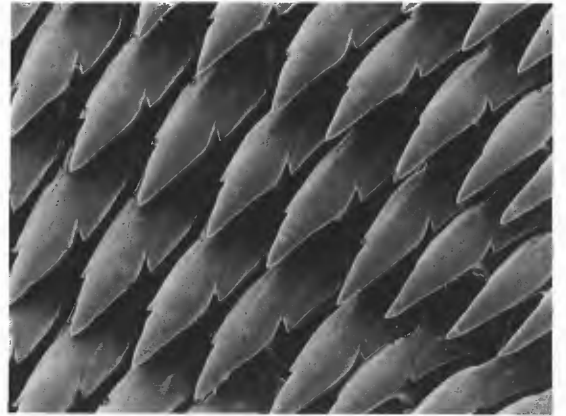
[M74] x650
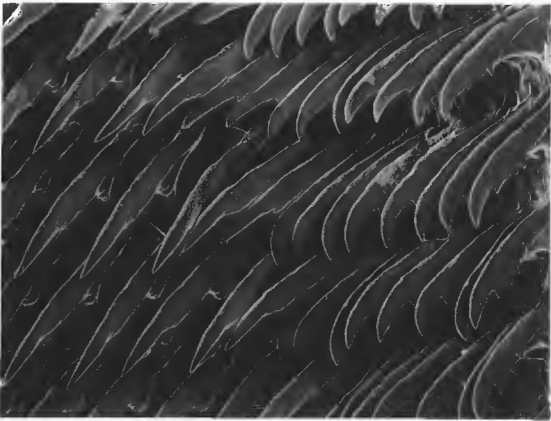
x990 [M75]
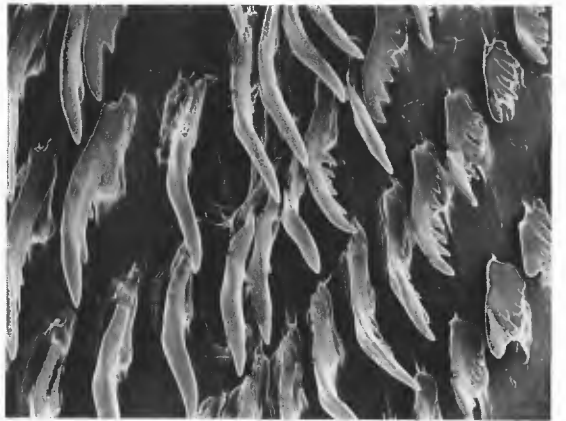
[M76] x1300
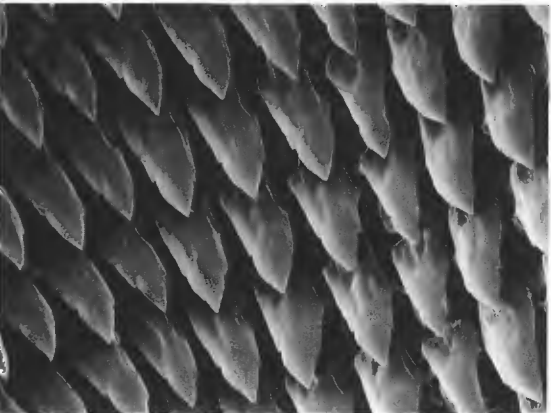
x750 [M77]
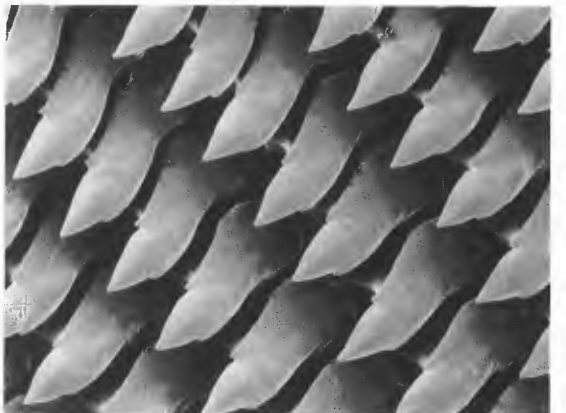
[M78] x1000

Fig. M73–78 Radular teeth: (73–76) *Lehmannia valentiana*; (77, 78) *Limacus flavus*.
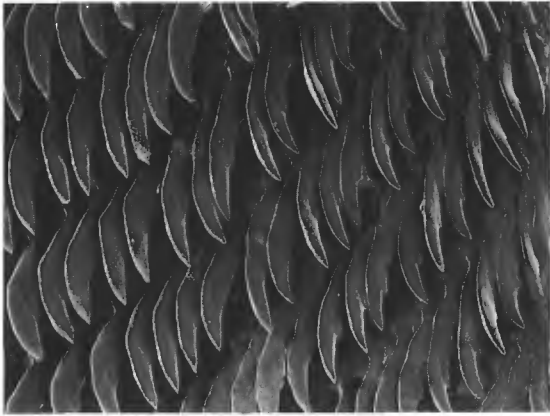
x750   [M79]
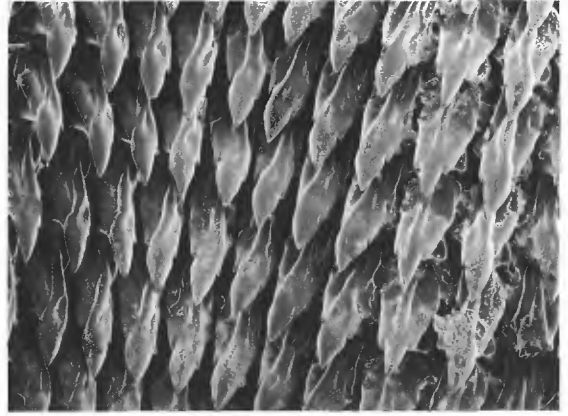
[M80]   x500
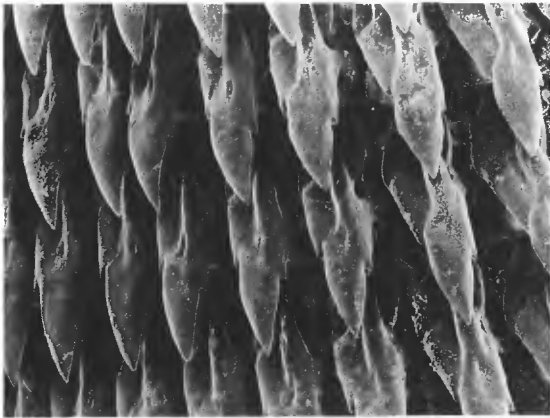
x500   [M81]

[M82]   x500
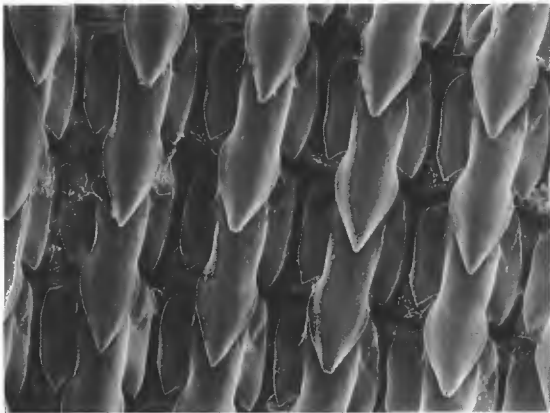
x560   [M83]
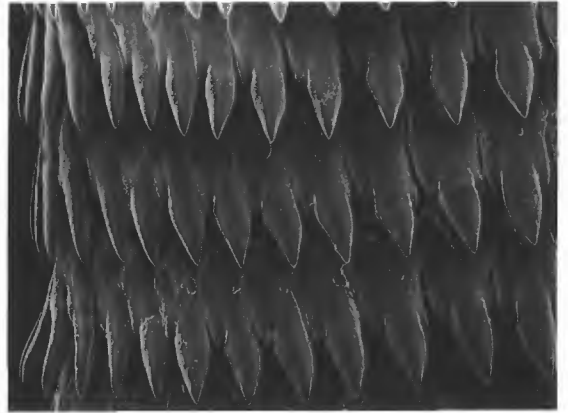
[M84]   x440

Fig. M79–84 Radular teeth: (79) *Limacus flavus*; (80–82) *Limax maximus*; (83, 84) *Milax gagates*.
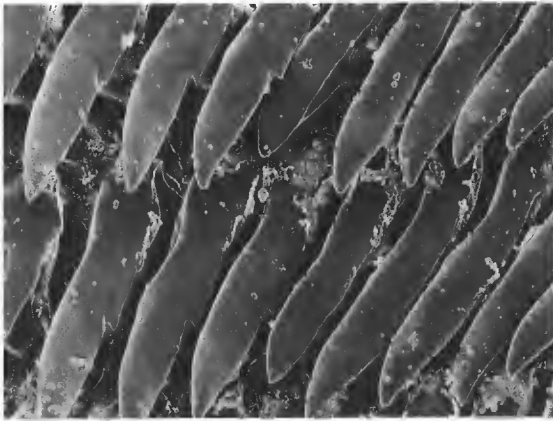
x1300   **[M85]**
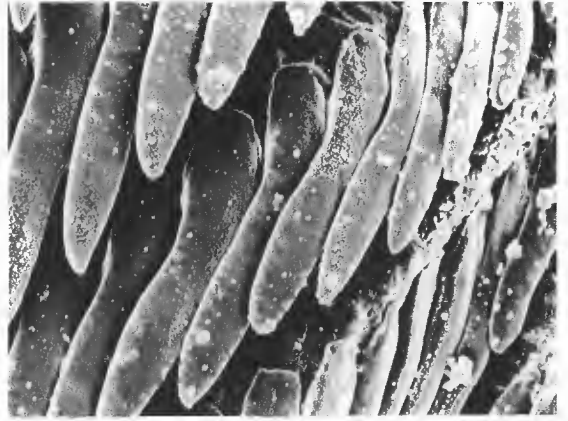
[M86]   x2100
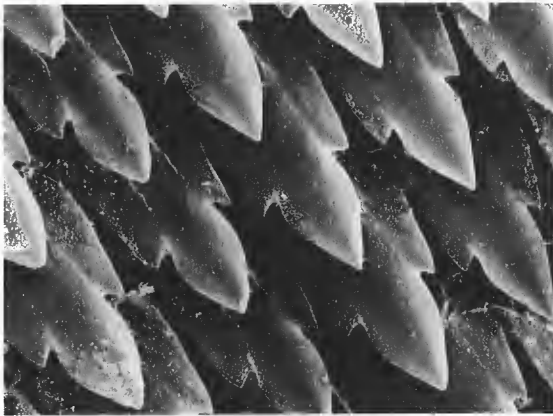
x1100   **[M87]**
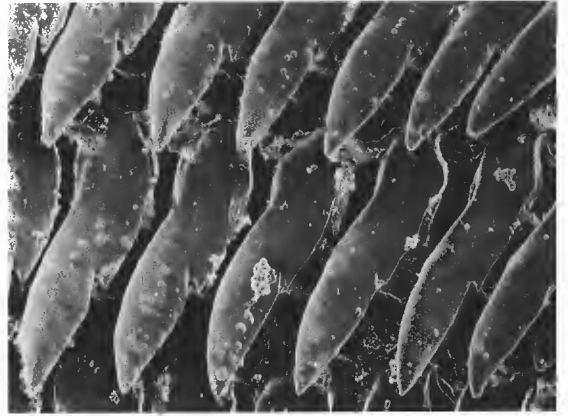
[M88]   x1300

x770   **[M89]**
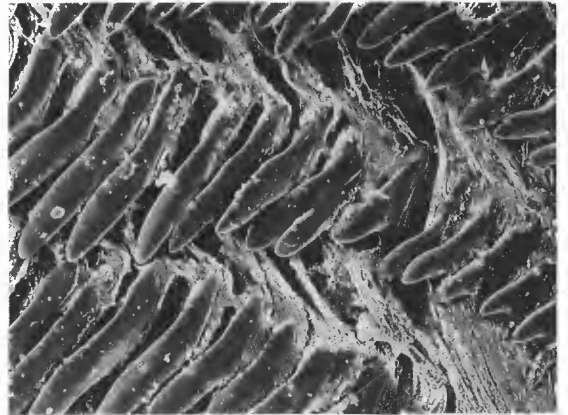
[M90]   x1300

Fig. M85–90 Radular teeth: (85, 86) *Milax gagates*; (87–90) *Tandonia budapestensis*.
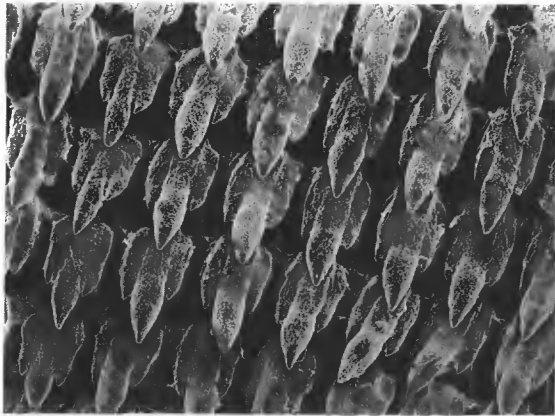
x440 [M91]
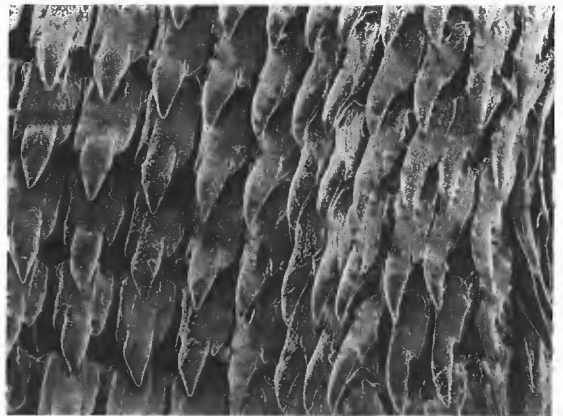
[M92] x440

x560 [M93]
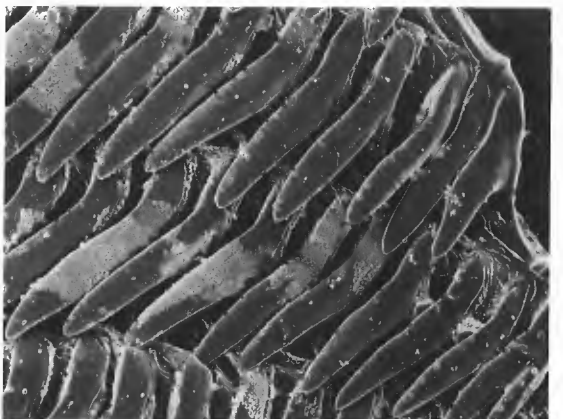
[M94] x1300
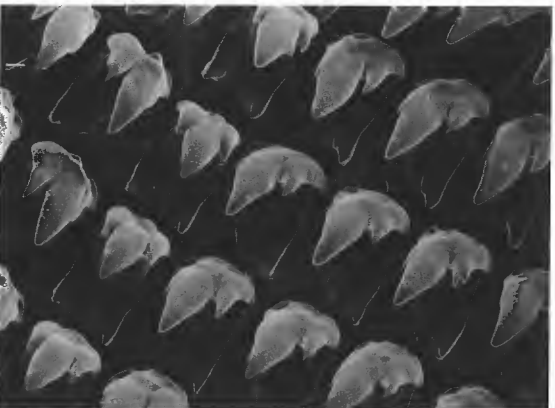
x1000 [M95]
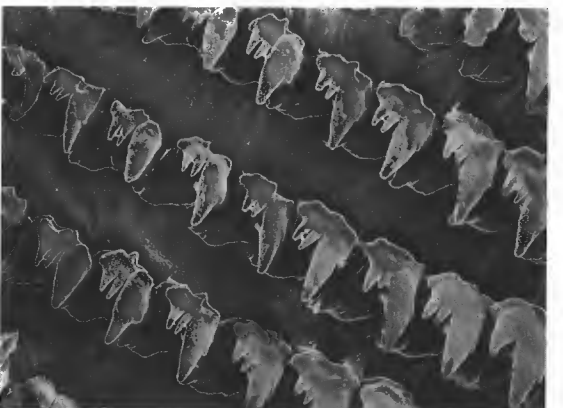
[M96] x1000

Fig. M91–96 Radular teeth: (91–94) *Tandonia sowerbyi*; (95, 96) *Lauria cylindracea.*
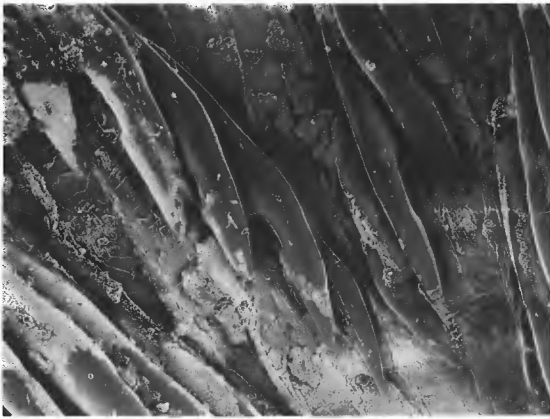
x440 [M97]

[M98] x170
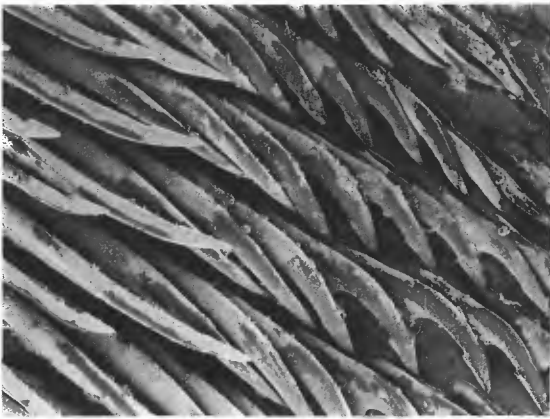
x110 [M99]
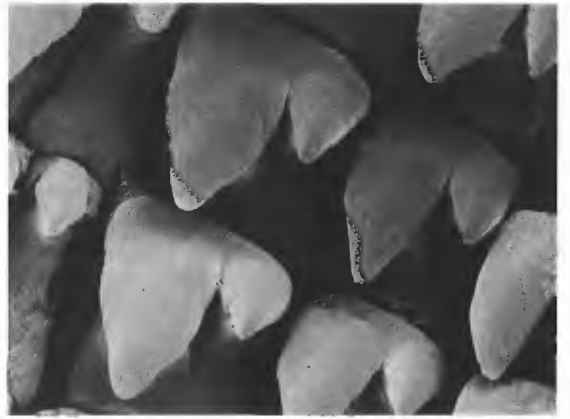
[M100] x5500

x6500 [M101]
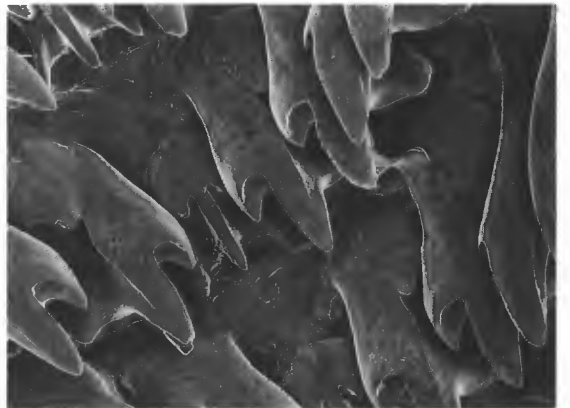
[M102] x880

Fig. M97–102 Radular teeth: (97–99) *Testacella haliotidea*; (100, 101) *Vallonia excentrica*; (102) *Oxychilus alliarius*.
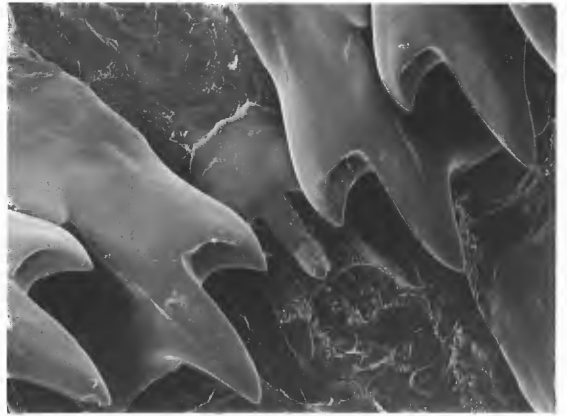
x850 [M103]

[M104] x1100

x350 [M105]
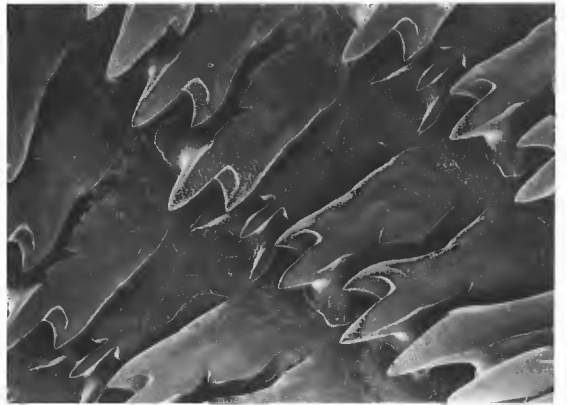
[M106] x550

x350 [M107]
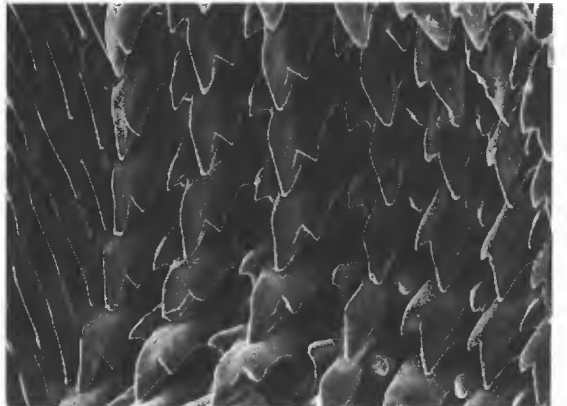
[M108] x2200

M103–108 Radular teeth: (103) *Oxychilus alliarius*; (104, 105) *O. cellarius*;
(106, 107) *O. draparnaudi*; (108) *Vitrea crystallina*.
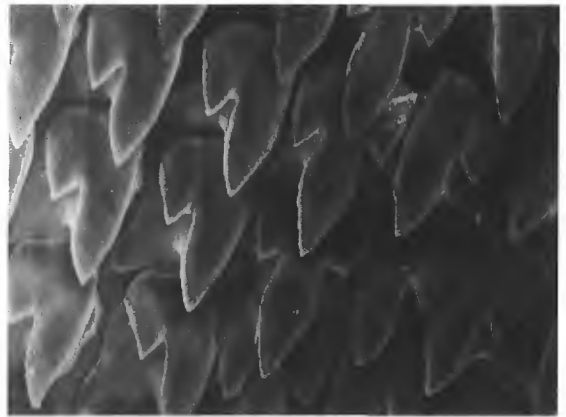
x2800   [M109]   [M110]   x2400
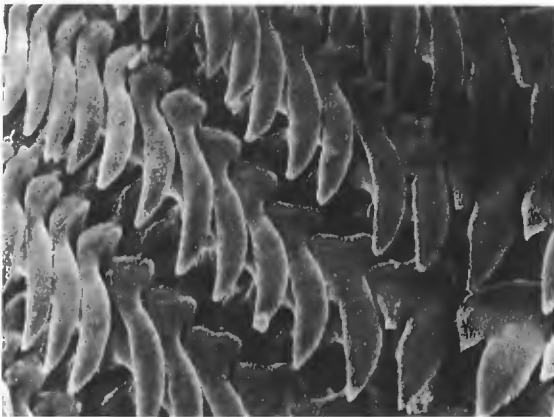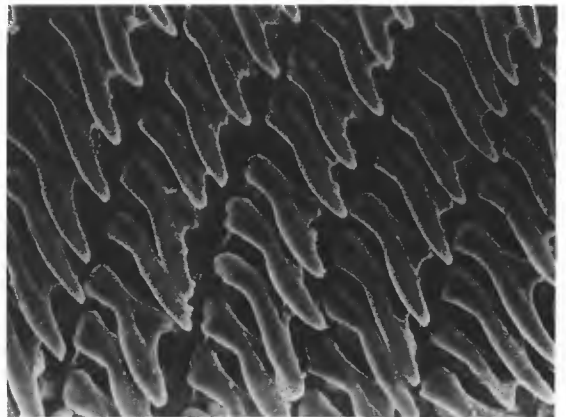
x2400   [M111]   [M112]   x2400
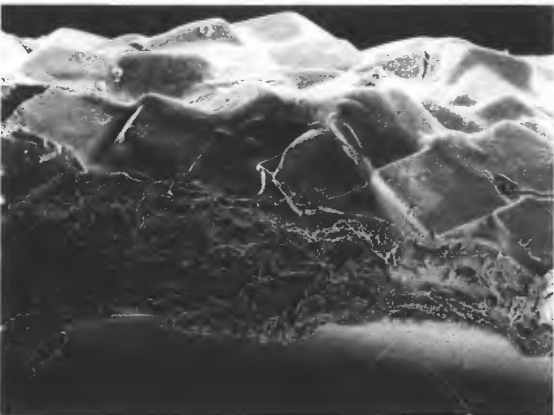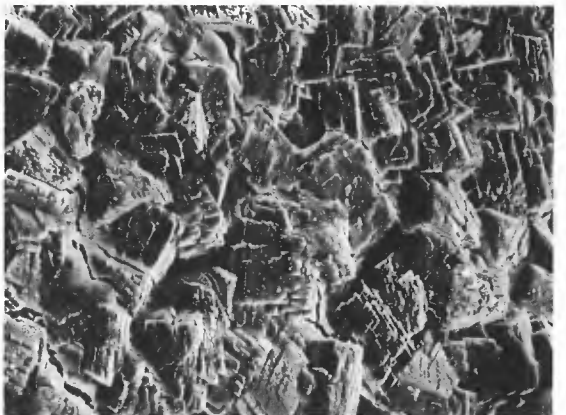
x1400   [M113]   [M114]   x3800

Fig. M109–112 Radular teeth: (109) *Vitrea crystallina*; (110–112) *Zonitoides arboreus*.
Fig. M113 Cross-section of egg shell, *Cochlicopa lubrica*. **Fig. M114** Surface of egg shell, *Coneuplecta calculosa*.
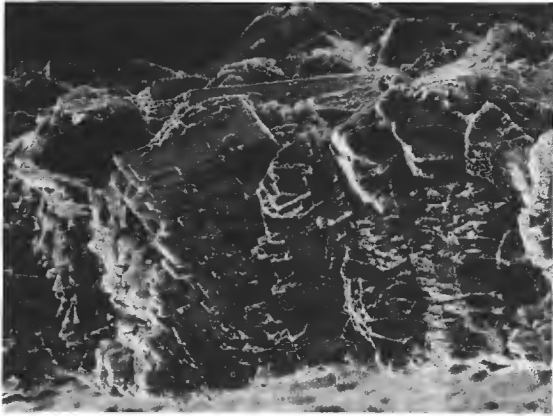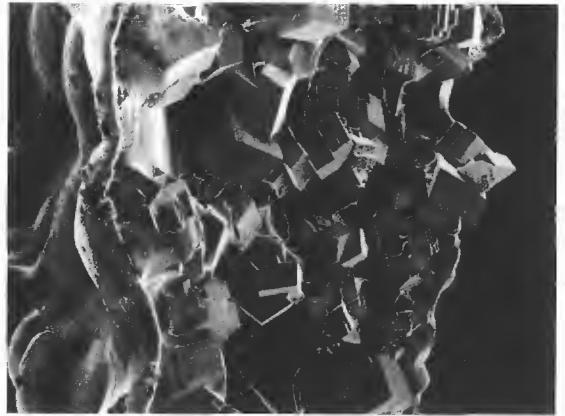
x5500   [M115]   [M116]   x1100
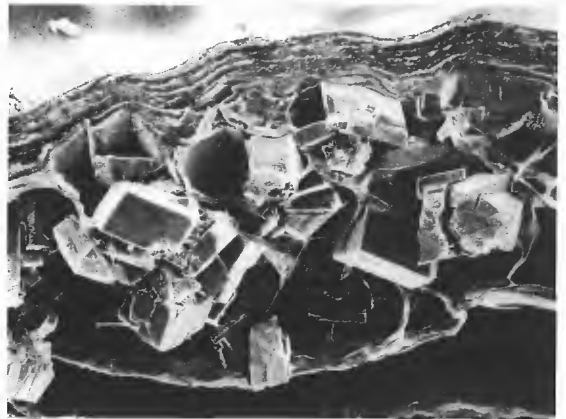
x2200   [M117]   [M118]   x2000

x770   [M119]   [M120]   x1200

Fig. M115, 116 Cross-section of egg shell, *Coneuplecta calculosa* and *Cantareus aspersus*.
Fig. M117–120 Surface and cross-section of egg shell: (117, 118) *Prietocella barbara*; (119, 120) *Vallonia excentrica*.
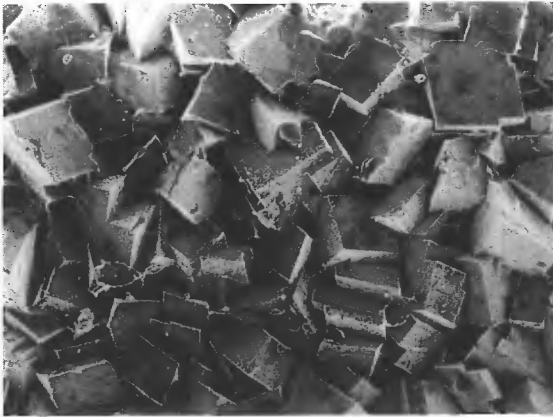
x1600   **[M121]**
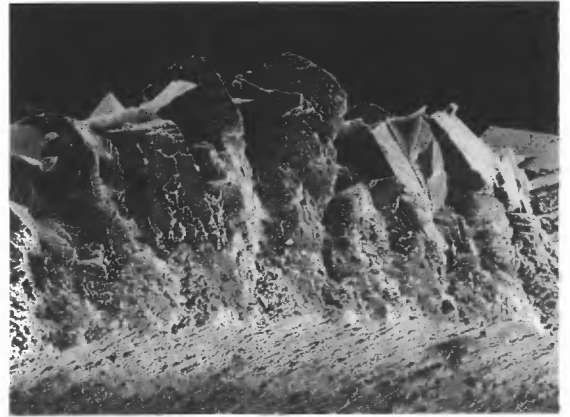
[M122]   x2000
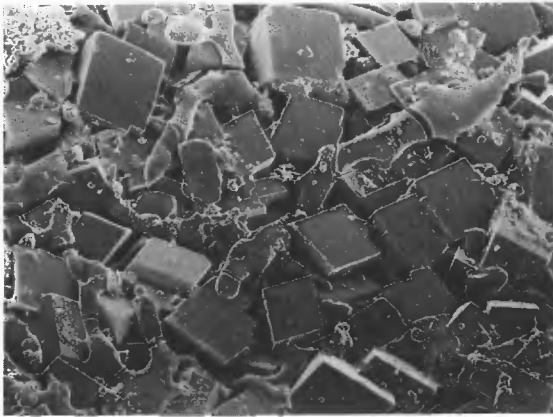
x1600   **[M123]**

[M124]   x2200
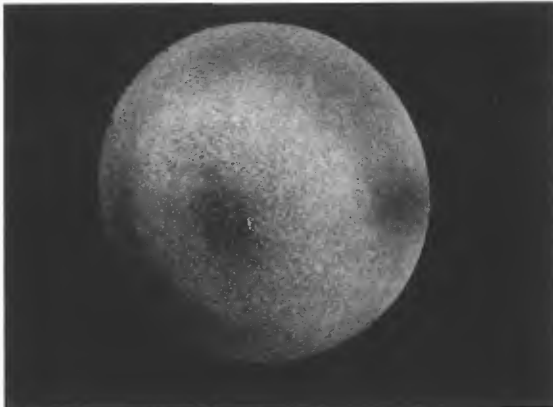
x80   **[M125]**
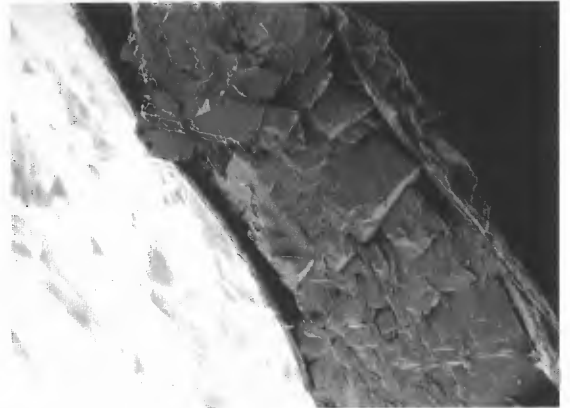
[M126]   x5000

Fig. M121–124 Surface and cross-section of egg shell: (121, 122) *Oxychilus alliarius*;
(123, 124) *O. cellarius*. **Fig. M125, 126** Egg and cross-section of shell, *Zonitoides arboreus*.

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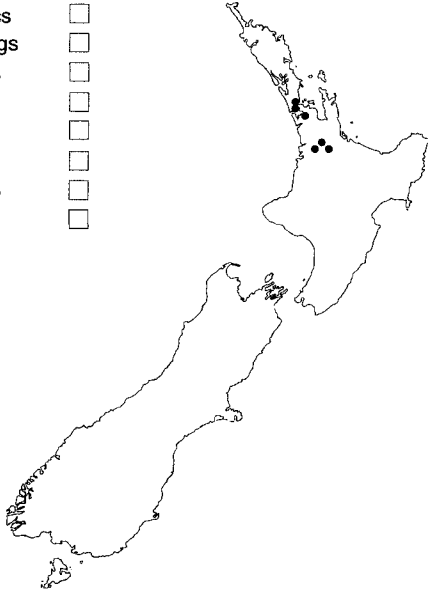
Map 1 Collection localities, *Deroceras laeve.*

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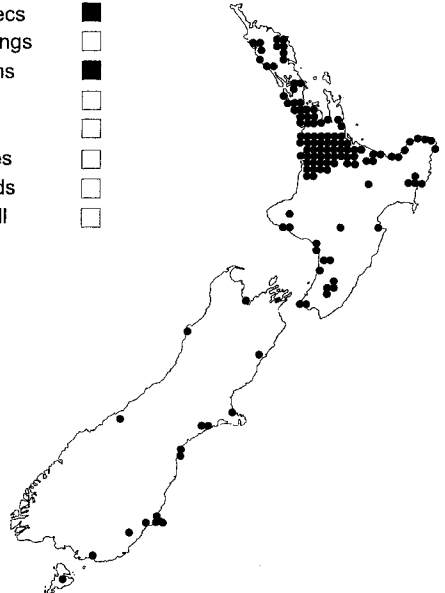
Map 2 Collection localities, *Deroceras panormitanum.*

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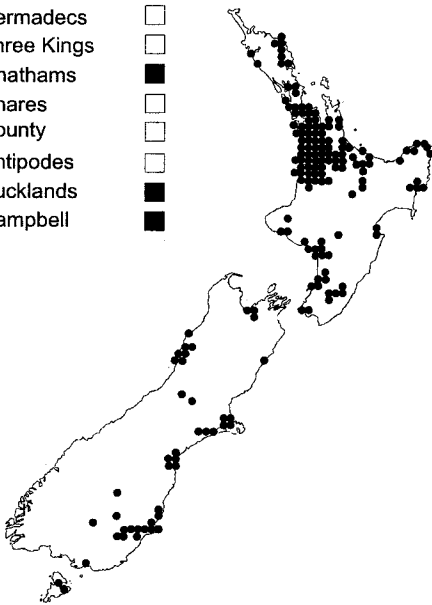
Map 3 Collection localities, *Deroceras reticulatum.*

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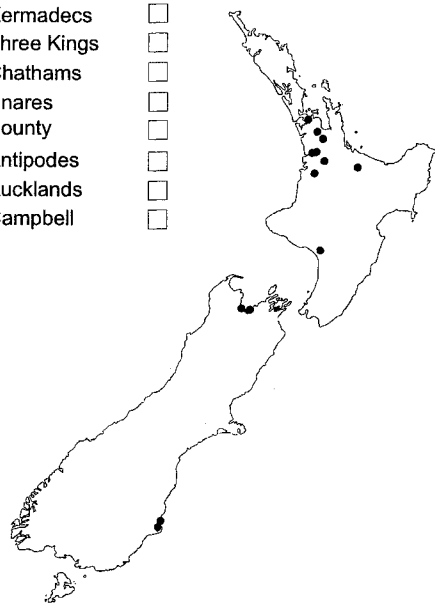
Map 4 Collection localities, *Arion distinctus.*

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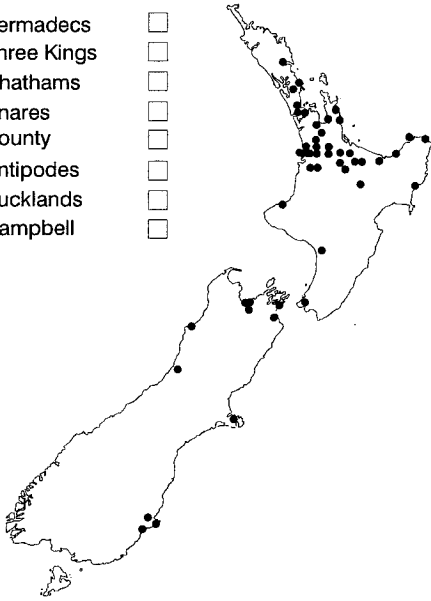
Map 5 Collection localities, *Arion hortensis*.

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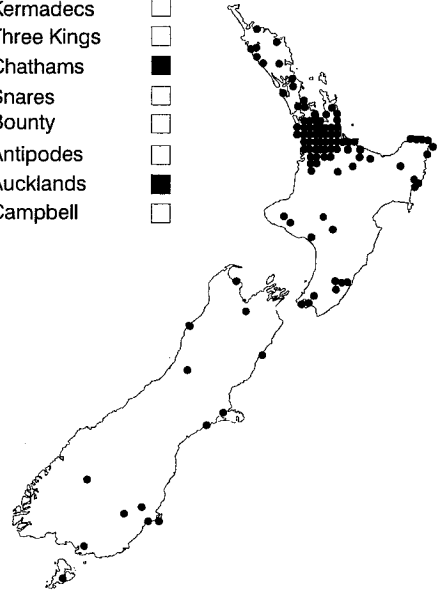
Map 6 Collection localities, *Arion intermedius*.

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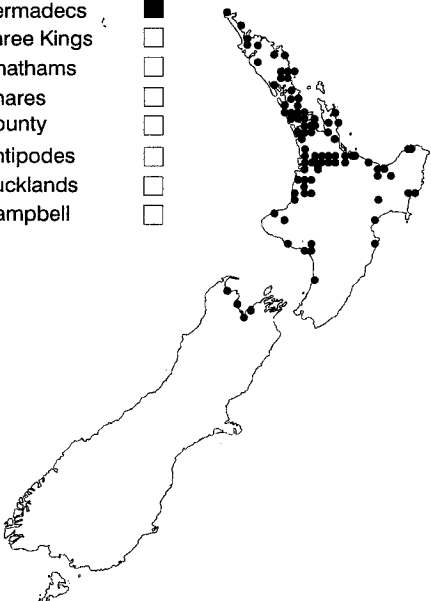
Map 7 Collection localities, *Cochlicopa lubrica*.

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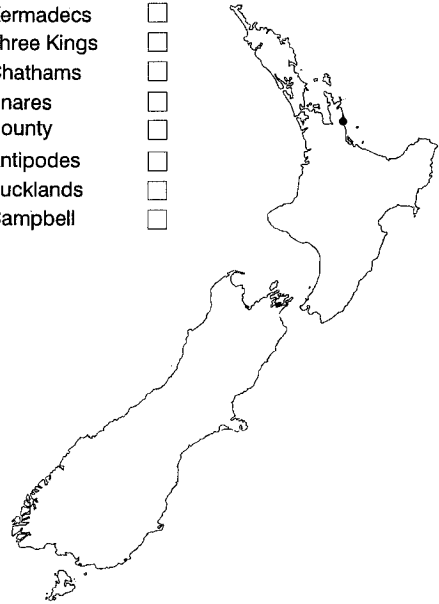
Map 8 Collection localities, *Coneuplecta calculosa*.
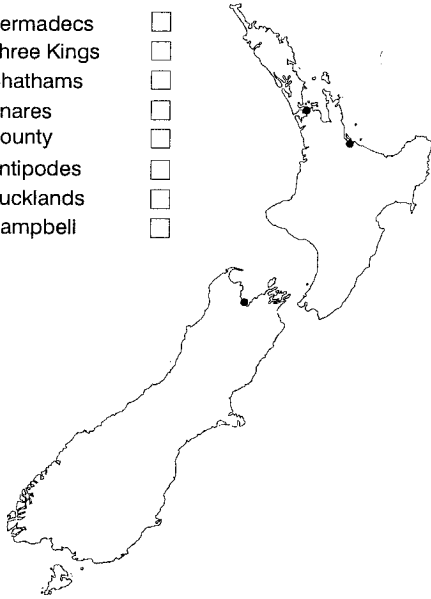
Map 9 Collection localities, *Cecilioides acicula*.
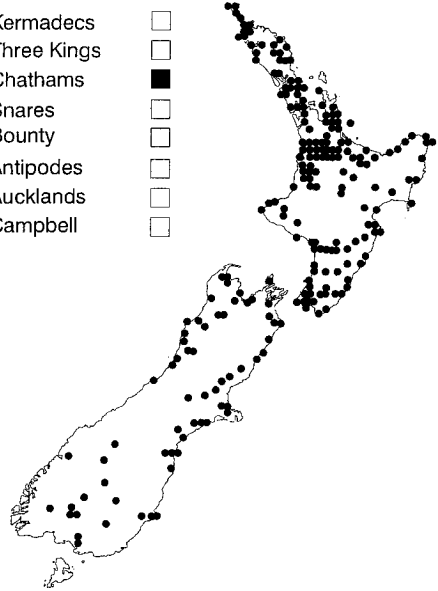
Map 10 Collection localities, *Cantareus aspersus*.
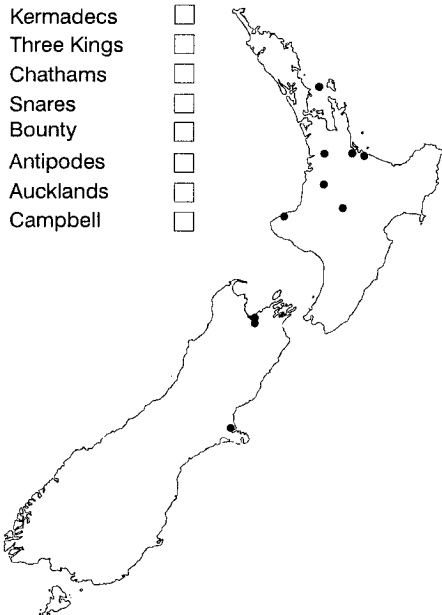
Map 11 Collection localities, *Helicodiscus singleyanus*.
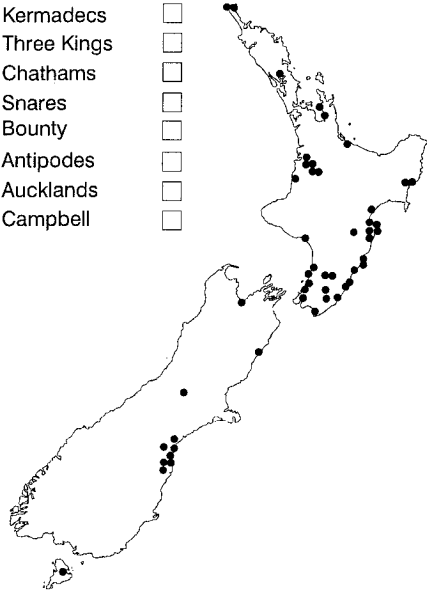
Map 12 Collection localities, *Candidula intersecta*.

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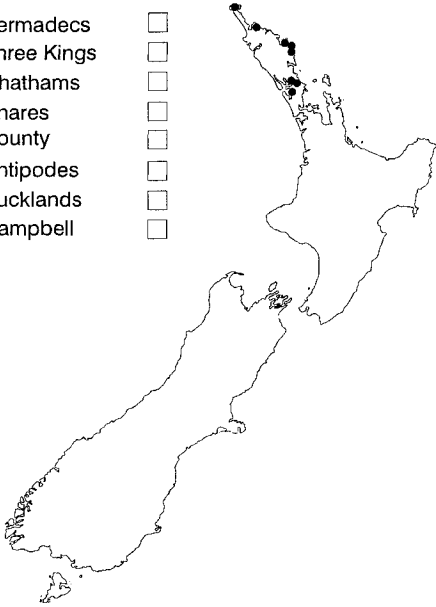
Map 13 Collection localities, *Prietocella barbara*.

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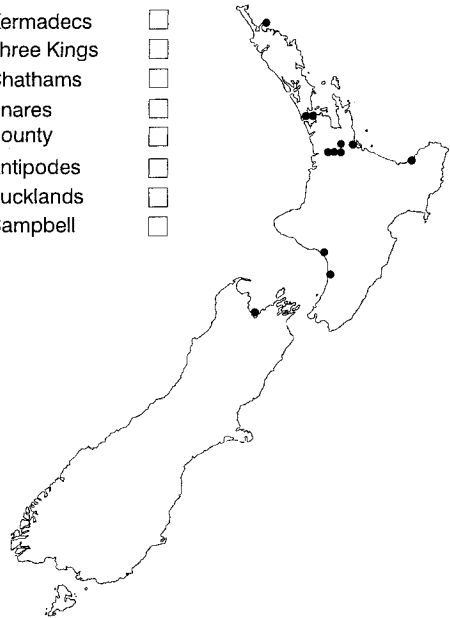
Map 14 Collection localities, *Lehmannia nyctelia*.

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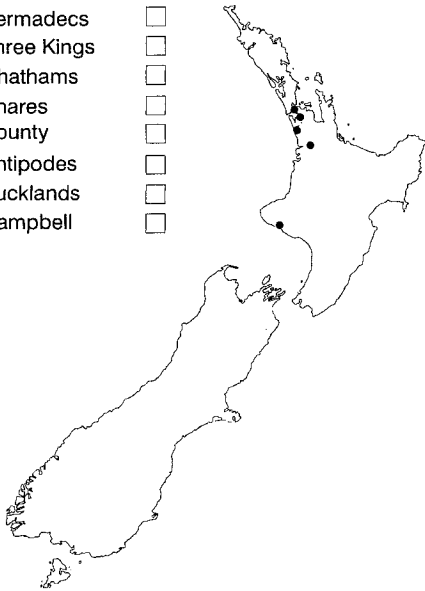
Map 15 Collection localities, *Lehmannia valentiana*.

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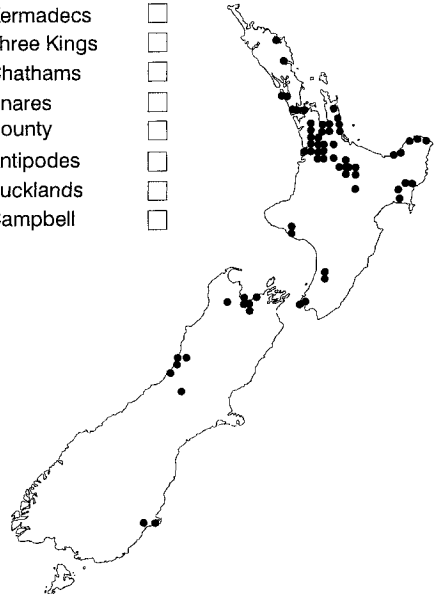
Map 16 Collection localities, *Limax maximus*.

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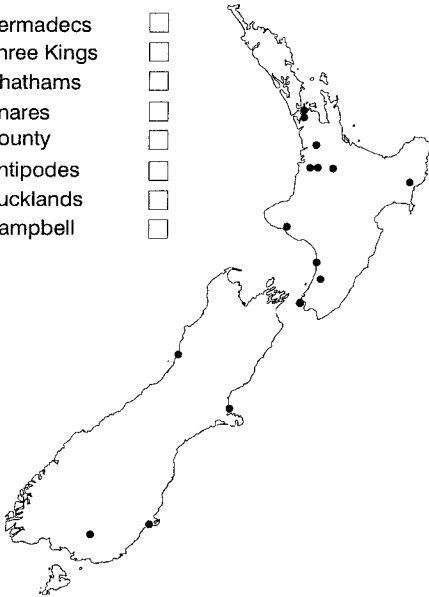
Map 17 Collection localities, *Limacus flavus*.

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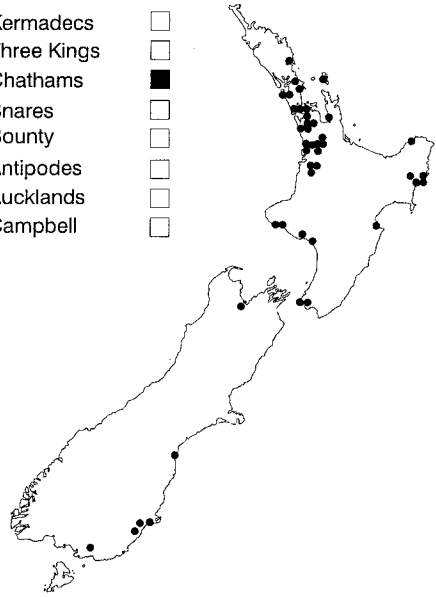
Map 18 Collection localities, *Milax gagates*.

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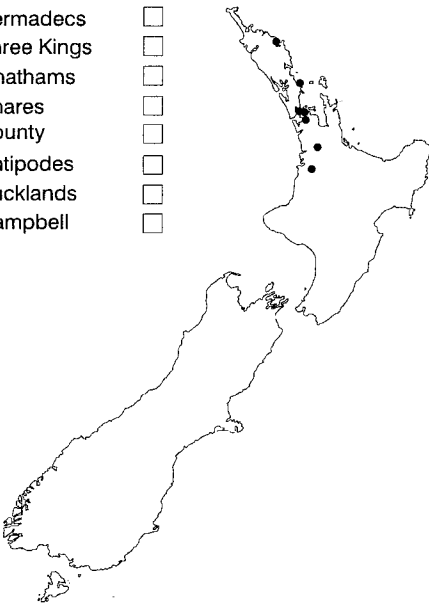
Map 19 Collection localities, *Tandonia budapestensis.*

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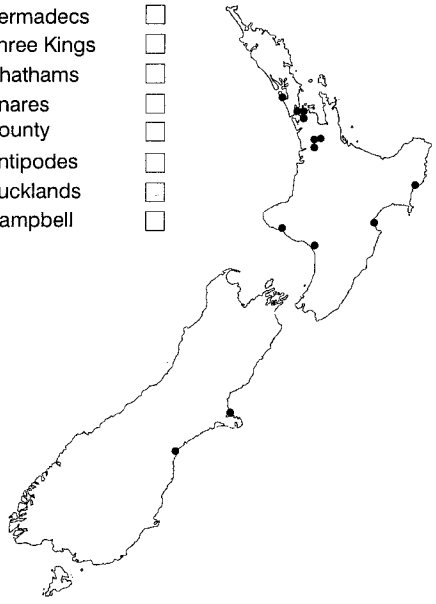
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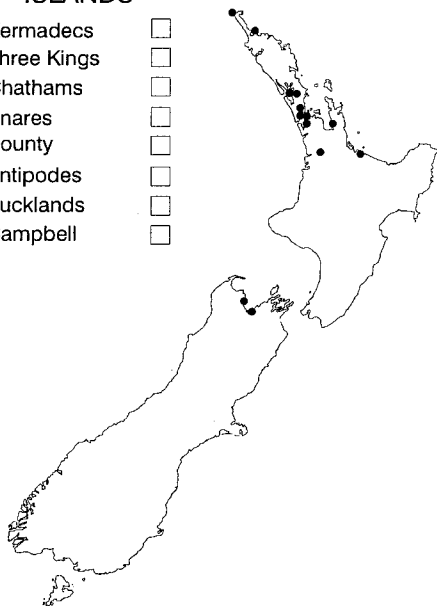
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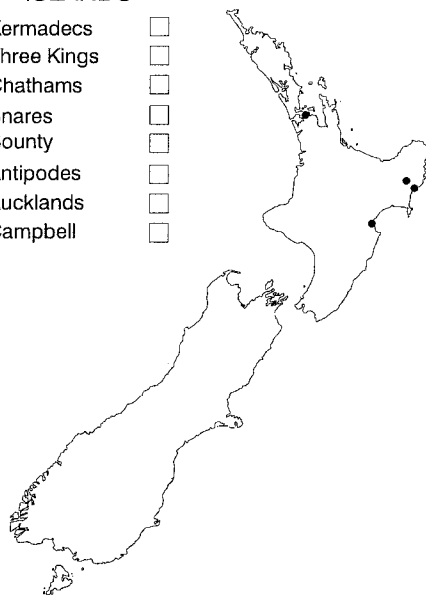
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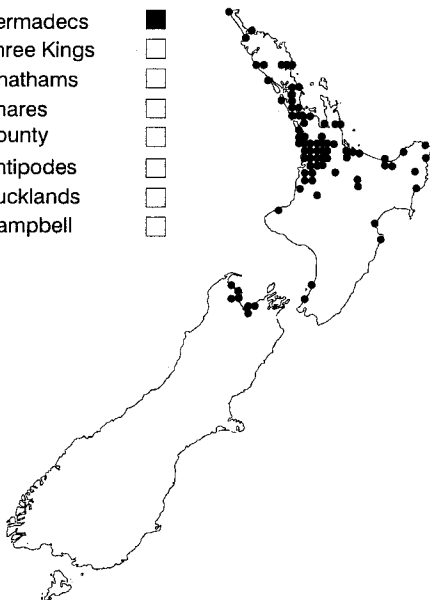
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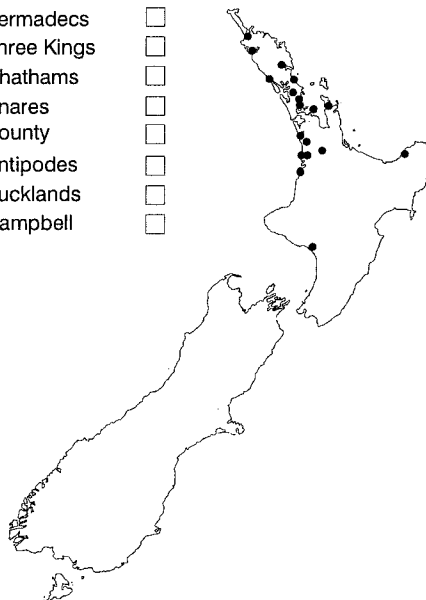
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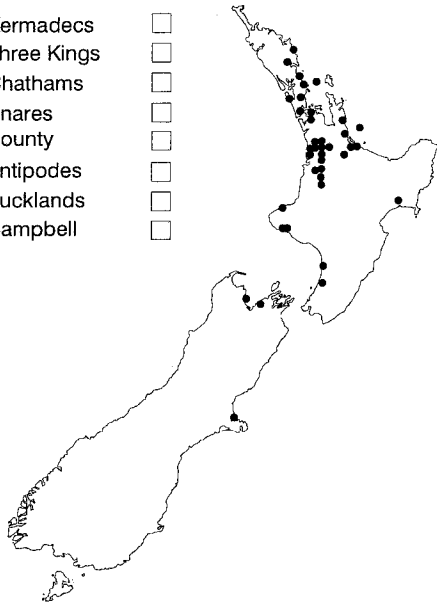
Map 25 Collection localities, *Oxychilus alliarius*.

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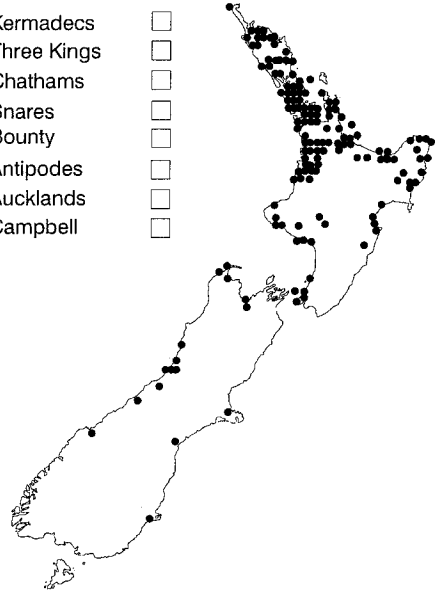
Map 26 Collection localities, *Oxychilus cellarius*.

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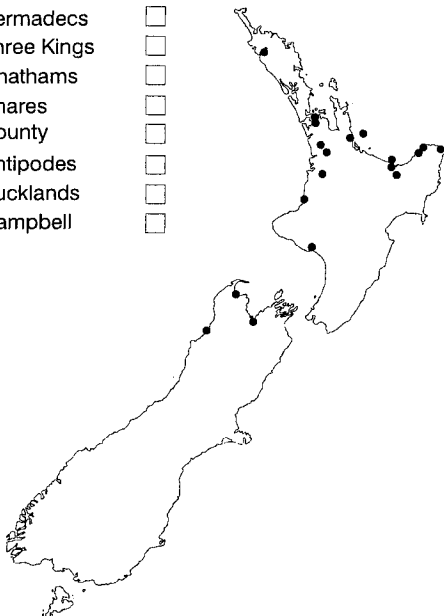
Map 27 Collection localities, *Oxychilus draparnaudi*.

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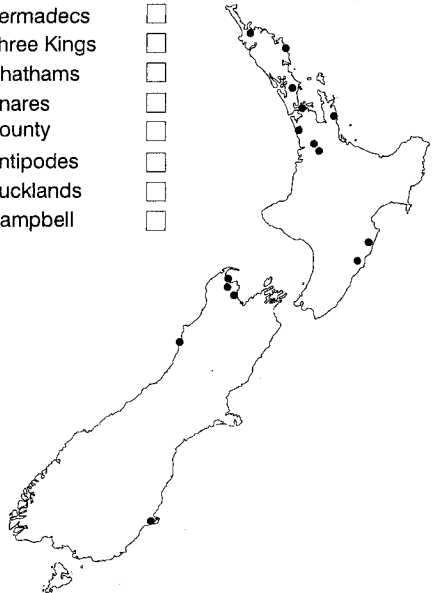
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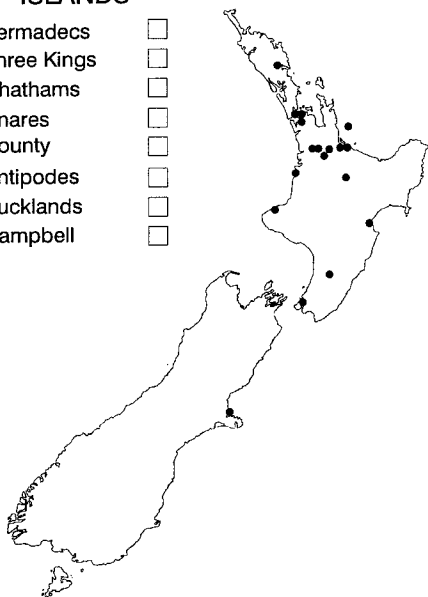
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TAXONOMIC INDEX

This index covers the nominal taxa mentioned in the text, regardless of their current status in taxonomy. In the case of synonyms, the combinations of generic and specific names listed are those originally published by authors, and may differ from combinations implicit in current usage. **Taxa in bold** indicate valid taxa which have a description in this publication, and **page numbers in bold** indicate the start page of a description. The letter "**k**" after a page number indicates the page of the key to the taxon. The Figures, Colour plates (prefixed "**C**"), SEM micrographs (prefixed "**M**"), and Maps are located on the following pages: **Figures**, pages 154–160 and 169–207; **Colour plates**, pages 161–168; **SEMs**, pages 208–228; **Maps,** pages 229–236.

North Island

AK	– Auckland
BP	– Bay of Plenty
CL	– Coromandel
GB	– Gisborne
HB	– Hawkes Bay
ND	– Northland
RI	– Rangitikei
TK	– Taranaki
TO	– Taupo
WA	– Wairarapa
WI	– Wanganui
WN	– Wellington
WO	– Waikato

South Island

BR	– Buller
CO	– Central Otago
DN	– Dunedin
FD	– Fiordland
KA	– Kaikoura
MB	– Marlborough
MC	– Mid Canterbury
MK	– Mackenzie

NC	– North Canterbury
NN	– Nelson
OL	– Otago Lakes
SC	– South Canterbury
SD	– Marlborough Sounds
SI	– Stewart Island
SL	– Southland
WD	– Westland

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Three Kings ☐
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Area codes and boundaries used to categorise specimen locality data (after Crosby *et al.* 1976)
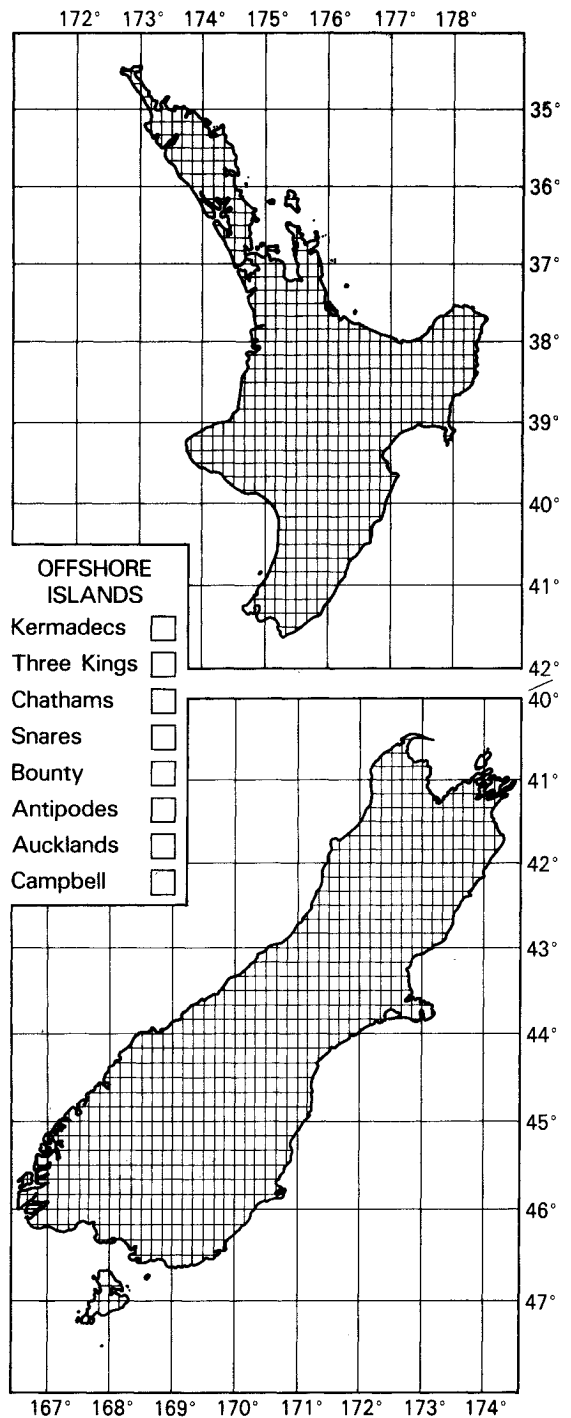
Base map for plotting collection localities; this may be photocopied without copyright release

Norfolk Island

30°S

Kermadec Islands

Lord Howe Island

S O U T H

Three Kings Islands

P A C I F I C

35°

T A S M A N

O C E A N

S E A

NORTH ISLAND

40°

SCALE
(km at 45°S latitude)

Chatham Islands

0   200   400

45°

SOUTH ISLAND

Stewart Island

The Snares

Bounty Islands

Antipodes Islands

50°

Auckland Islands

Campbell Island

THE NEW ZEALAND SUBREGION

(excludes Lord Howe, Norfolk, and Macquarie islands except in the context of extralimital zoogeography)

Macquarie Island

55°S

160°E   165°   170°   175°   180°   175°W

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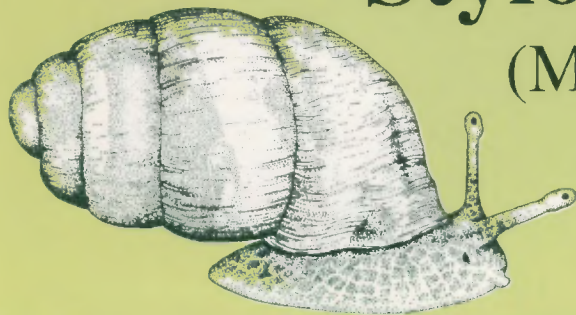# Fauna of New Zealand

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Number 38

Naturalised terrestrial Stylommatophora
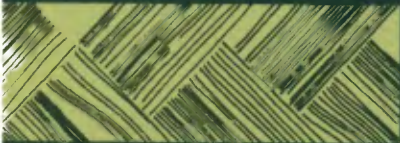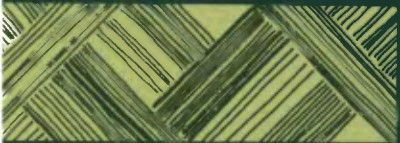
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Gary M. Barker